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I

INTRODUCTION

Widespread species of plants must cope with a wide range of environmental conditions in order to maintain their far-flung boundaries. Restricted endemics, on the other hand, are unable to meet such a test, since they survive only in a much narrower environmental range. Widespread species meeting the demands of diverse environments consist of series of ecologic races. These races were first studied experimentally by Turesson (1922), who named them ecotypes, a term and concept universally accepted.

The following chapters are devoted to an experimental analysis of a series of ecotypes of the *Achillea millefolium* complex from climatically contrasting regions, and these ecotypes will be referred to as climatic races. The objectives of this study have been to clarify the relations of the individual to the local population, of the local population to the climatic race, of the climatic race to the species and the species complex, and to extend our knowledge of the relationships between plants and their environments, thereby advancing our understanding of the evolutionary processes giving rise to these natural units. Aspects left unexplored in the less intensive transplant studies reported by the writers in 1940 are here investigated in more detail, with the result that the nature of ecotypes, or climatic races, is correspondingly clarified.

The members of the *Achillea millefolium* complex almost blanket the temperate and subarctic regions of the Northern Hemisphere. In occupying such a diversity of climates, this complex has evolved an exceptionally complete set of races, making it a unique experimental subject. For example, its forms occur almost without interruption across central California in all its major environments from the shores of the Pacific, over the floor of the hot, dry interior Great Valley, to near the crest of the Sierra Nevada at 11,000 feet, and eastward across the Great Basin. They extend eastward to the Atlantic, southward to Mexico, and northward to Alaska and the western tip of the Aleutian chain. Although most of the experimental material in the present studies came from western America, some European material has been included for comparison. All Achilleas are hardy, rhizomatous perennials that are easily handled.

The *Achillea millefolium* complex is sometimes considered by conservative taxonomists to contain but one polymorphic species. This view has some support in that the series of variations within the complex have no major morphological breaks, but consist of trends that seem to be indissolubly linked together by finely graded morphological steps.

The Old World *Achillea millefolium* L. and the two New World species, *A. borealis* Bong. and *A. lanulosa* Nutt., are separated by trivial

morphological characters of leaf cut and vesture that ordinarily would be considered quite insufficient to mark distinct species. The two North American species, however, are separated by the difference in their number of chromosomes, for the more inland and eastern species, *A. lanulosa,* is tetraploid, with $n=18$, whereas the West Coast species, *A. borealis,* is hexaploid, with $n=27$ chromosomes. The latter, in turn, apparently does not come in contact with the Eurasian hexaploid, *A. millefolium,* for their ranges do not overlap, and so the small morphological distinctions between them assume added importance.

The general relationships and taxonomy of this group of perennial herbs have already been discussed by the authors (1940). In brief, *A. millefolium* L. is considered to be native only in the Old World. This hexaploid species has doubtless been introduced along the eastern seaboard of the United States, but is probably more limited there than one would be led to believe by the manuals, for Turesson's chromosome counts of five different populations in the northeastern tier of states from North Dakota to Vermont and Nova Scotia disclosed only tetraploids, with $n=18$ chromosomes. This and all other tetraploid material is referred to the widespread mid-continental *A. lanulosa* Nutt., which extends from New England across the Great Plains and the Rocky Mountains to the west coast, where it is replaced by a second hexaploid, *A. borealis* Bong.

The distribution of the two species in western North America is as follows: *A. borealis,* the hexaploid, extends from the western tip of the Aleutians to at least southern Alaska, thence southward along the coast to southern California. The typical form is coastal Alaskan; the maritime ecotype, which has been traced from the coast of northern Oregon to that of San Luis Obispo County, California, is referable to ssp. *arenicola* (Heller) Keck; the form in the Sierran foothills and in the Coast Ranges from northern California southward at least as far as Santa Barbara County is known as ssp. *californica* (Poll.) Keck. The giant form in the San Joaquin Valley bottoms, which has been named *A. gigantea* Poll., is probably but another subspecies of *A. borealis.*

The tetraploid species, *A. lanulosa,* occurs east of the hexaploid, and the boundaries of the two appear to overlap here and there. In Oregon, *lanulosa* comes close to the coast, actually reaching it at Port Orford, where, like the hexaploid species, it has evolved a maritime ecotype. In California it recedes farther inland to the western flank of the Sierra Nevada, but to the south is found nearer the coast again in western Riverside County. Only two named forms are recognized: ssp. *typica,* the widespread form at lower and middle altitudes, and ssp. *alpicola* (Rydb.) Keck, the small-leaved form at high altitudes.

Where these species meet, their morphological similarity is so great that they can be distinguished by chromosome number only. Thus only approximations of the two ranges can be given because the cytological survey is not yet complete. On the western side of the continent the chromosome number is unknown of forms from such critical regions as the interior of Alaska, far northern Canada, coastal southern California, Lower California, and other states of Mexico. The situation has been greatly clarified, however, by the cytological investigations of W. E. Lawrence (1947), who has given a picture of the boundaries of these species as established by counts of over 100 different collections from the wild. The reader is referred to Lawrence's paper for a more detailed account of the cytological situation in these species.

EXPERIMENTAL FACILITIES AND PROCEDURE. The experimental gardens established by the Carnegie Institution of Washington at Stanford University at 30 m. altitude, at Mather on the western slope of the Sierra Nevada at 1400 m., and in Slate Creek Valley just east of the Sierran crest near timber line at 3050 m. were utilized in this study. The last-named garden, because of its situation, is generally referred to as Timberline Station. The three are arranged along the line of a transect across central California from which many of the races utilized in this study were taken. These stations and their environs have been more fully described by the writers in an earlier publication (1940).

In the present study, populations from widely different natural habitats were compared as they grew side by side in a uniform garden at Stanford, and also, for fourteen key populations, as they responded to transplanting to uniform gardens in three very different climates. These comparisons brought out both the genetic variation among plants from each locality and the racial differences among plants from different environments. All records and data refer to individual plants, whose identities were carefully preserved throughout the experiments. The populations from a wide array of habitats could thus be compared with respect to their differences in terms either of individual plant performance or of population averages.

The materials used in this investigation were seedling cultures representing wild populations chosen to cover a wide segment of the variation to be found in the *Achillea millefolium* complex. These plants are obligatory cross-pollinators, and, in collecting seed, effort was made to obtain it from a number of individuals at each locality in order to make the samples representative of the natural variation.

The seeds were sown in the greenhouse at Stanford, and random samples of usually 60 seedlings were pricked into flats and transferred

to the garden. The seedlings were planted in rows spaced 1 m. apart each way and grown to maturity. At the end of the second year, or in the case of some populations at the end of the first year, 30 individuals representing the entire range of variation among the 60 were selected for clonal division for the transplant experiments. Propagules of each individual were then grown simultaneously at the Stanford, Mather, and Timberline transplant gardens, one at each place. For three consecutive years annual records were taken from each propagule on printed forms listing the pertinent data designed to describe the performance of the plant in reasonable detail. Measurements were made showing the extent of growth, and notes were taken on the various phases of seasonal activity, such as the time of inception of growth, flowering, and dormancy. Herbarium specimens were preserved for later study. All these data were utilized in comparative study of the performance of each race at each of the three transplant stations. Special methods used in the study of growth of selected individuals in the controlled greenhouses at the California Institute of Technology are described in chapter IV.

In chapter II the races employed and the climates from which they came are described, and characteristics of the races as expressed in the uniform garden at Stanford are discussed and compared. In chapter III the reactions of certain key races at the three altitudinal transplant stations are compared; in chapter IV the growth of selected individuals of these races under controlled conditions is described as a step toward the understanding of the physiological differences between races. Finally, in chapter V, the present status of the study of ecotypes in plants is reviewed in the light of all the evidence.

II

COMPARISON OF POPULATIONS AT STANFORD

A first step toward discovering the climatic races in a group of plants is to compare series of populations from different climates in one uniform environment. A provisional analysis of the races can be made by observing their differences in response to such an environment. The lowland station at Stanford University, located in the winter rain belt of the warm temperate zone, is well adapted for this preliminary analysis. There is sufficient frost during the winter to bring to expression the winter dormancy of plants from cold climates, and sufficient heat during the dry summer to differentiate the summer-dormant forms coming from warm, dry climates. On the other hand, the climate is mild enough to permit continuous growth of forms from mild, equable climates. Achilleas from some eighty localities, mainly in western North America, differing greatly in altitude, latitude, and distance from the sea, have been grown and studied in the gardens at Stanford.

POPULATIONS FROM A TRANSECT ACROSS CENTRAL CALIFORNIA. Figure 1 shows typical representatives of races of *Achillea* from a transect across central California that have been grown in the same environment, the gardens at Stanford. Each plant represents a population whose habitat is indicated on the profile of the transect by an arrow. The frequency graph at the upper right of each specimen, drawn to the scale shown, indicates the range of variation in height of individuals within that population. The height of each plant illustrated is equal to the statistical mean of its population, indicated by the arrow above the specimen.

It is clear from figure 1 that there are striking differences between the populations of *Achillea* from very different habitats and altitudes along the transect, but that populations from adjacent habitats are more alike. In fact, in every case they overlap with respect to height.

The single character of height was selected in figure 1 to represent the differences between the races because it was easily measured and graphed. But there are many other characters, both morphological and physiological, that distinguish these populations. Some are of importance for the survival of the race, though others appear to represent random variation without ecological significance. Many characters have been studied, and their relative importance will be considered in the following pages. The races from the transect across central California and a few that have been studied intensively from other latitudes will be emphasized.
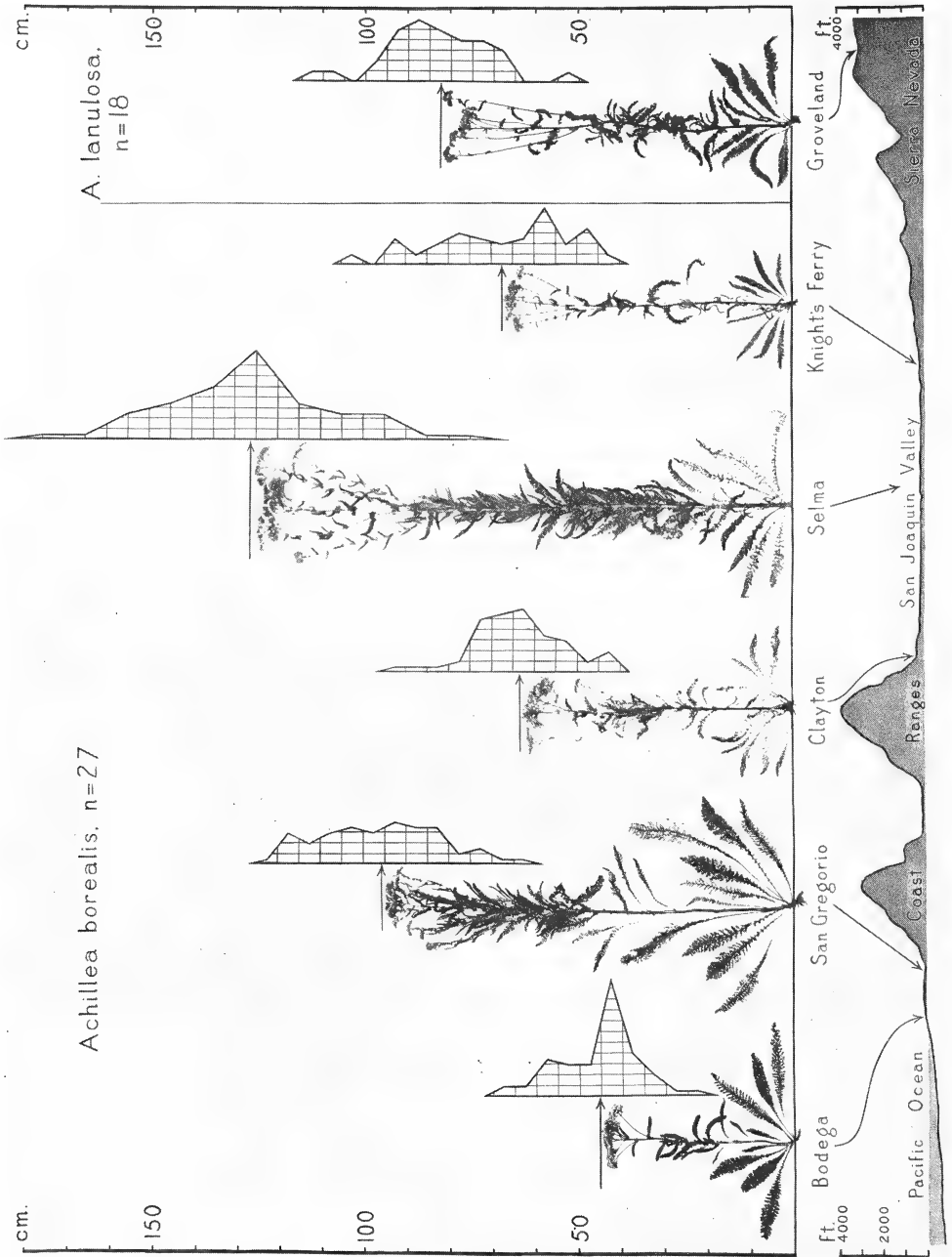
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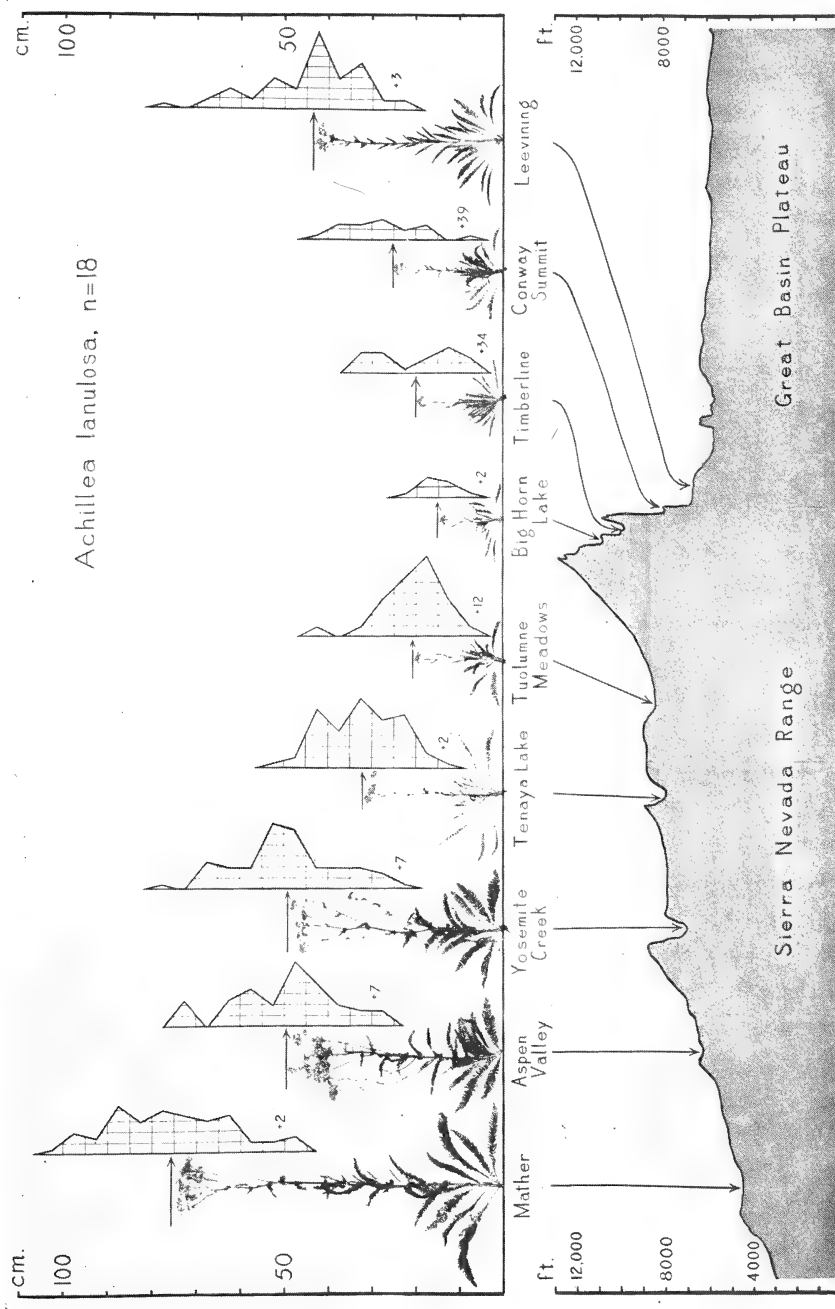
FIG. 1. Representatives of populations of *Achillea* as grown in a uniform garden at Stanford. These originated in the localities shown in the profile below of a transect across central California at approximately 38° north latitude.

Above: the western half of the transect, starting at the Pacific Coast; below: the eastern half, extending to the Great Basin plateau; the two parts together represent an air-line distance of about 200 miles. Altitudes are to the scale shown in feet. Horizontal distances are not to scale.

The plants are herbarium specimens, each representing a population of approximately 60 individuals. The frequency diagrams show variation in height within each population: the horizontal lines separate class intervals of 5 cm. according to the marginal scale, and the distance between vertical lines represents 2 individuals. The numbers to the right of some frequency diagrams indicate the nonflowering plants. The specimens represent plants of average height, and the arrows point to mean heights.

In table 1 are listed all the cultures of *Achillea* that were grown at Stanford. Starting from central California, these are arranged in geographical groups and according to chromosome number or degree of ploidy, the tetraploids (4n) having 36 chromosomes, and the hexaploids (6n), 54. Culture numbers, origin, height of stems, earliness of flowering, and general type of seasonal periodicity are indicated for each. The cultures from key locations that were studied most intensively are marked with an asterisk (*).

Neither the figure nor the table portrays all the significant characteristics of the populations, hence a discussion of the more important features of each key population is given below. Special attention is paid to the relation between the characteristics of each population and the environment, particularly climate.

CLIMATES OF THE CENTRAL CALIFORNIA TRANSECT. The localities on the 200-mile transect represented in figure 1 have unusually contrasting climates. Their climates differ in seasonal temperatures, in the diurnal spread between maximum and minimum temperatures, and in the amount and distribution of precipitation. These characteristics can be described by curves. Figures 2 to 5 show both the average and the extreme maximum and minimum monthly temperatures for stations along the California transect. The average monthly precipitation and average length of growing season are also indicated.

At Point Reyes, some 30 miles northwest of San Francisco on the exposed coast, the ocean has a marked buffering effect on air temperatures, as appears in figure 2. The strikingly small diurnal variation is represented by the proximity of the curves for average maximum and minimum temperatures, and the slight variation between seasons is indicated by the flatness of the curves. There is almost no frost during the entire year, thus there is an almost continuous growing season.

At Palo Alto, near the Stanford garden, only 14 miles from the ocean but separated from it by an arm of the outer Coast Range, daily and seasonal temperature variations almost treble those of Point Reyes. Here, the growing season measured by the frost-free period is shorter, but the cooler winter weather is not severe enough to prevent active growth in such herbaceous perennials as *Achillea*. In fact, this plant uses the cool winter rainy season for active vegetative growth. The dry summer and fall periods check its growth entirely unless it is irrigated.

The climate is more continental in the San Joaquin Valley east of the inner Coast Range, the summer temperatures are much higher than those

TABLE 1

CULTURES OF ACHILLEA AT STANFORD

| Geographical region	Ploidy		Number and origin	No. of plants	Longest stems (cm.)	First flowers	Dormancy
Central California coast (38° 20' to 35° 15' N. lat.)	6n	*3776	Bodega coast, 8 m.	59	45.3±1.23	May 21.1	none
		3775	San Francisco, 12 m.	63	62.5±1.07	Apr. 20.3	
		3773	Salada bluffs, 180 m.	63	65.4±1.37	May 5.6	
		3768	Montara coast, 5 m.	59	73.5±1.34	May 19.5	
		3769	Montara Mtn., 30 m.	58	75.0±1.61	May 14.4	
		3770	Montara Mtn., 30 m.	62	77.2±1.04	May 12.9	
		3771	Montara Mtn., 30 m.	62	91.3±1.36	May 12.3	
		3772	Montara Mtn., 30 m.	54	96.8±1.46	May 15.5	
		3363	Tunitas, bluffs, 60 m.	4	87.5±4.18	May 4.2	
		3364	Tunitas, forest, 20 m.	3	87.3±2.90	Apr. 29.0	
		*3777	San Gregorio, 50 m.	59	95.8±2.12	May 7.8	
		3361	Año Nuevo Pt., 3 m.	10	75.2±4.15	Apr. 27.1	
		3360	Seaside, 4 m.	9	84.6±2.5	Apr. 26.9	
		2458	Asilomar coast, 6 m.	3	89.7±2.64	June 8.6	
		3381-11	Cambria coast, 5 m.	1	58	May 5	
		1820-1	Morro Rock, 3 m.	1	80	May 30	
		3381-21	San Luis Obispo, 30 m.	1	84	May 18	
		3381-32	Nojoqui Pass, 275 m.	1	67	May 8	
Central California foothills (39° 8' to 37° 50' N. lat.)	6n	3964	W. of Williams, 550 m.	59	81.5±1.51	Apr. 22.5	summer
		*3965	Clayton, 210 m.	57	63.4±1.42	Apr. 12.8	
		3379	Stanford, 30 m.	5	79.0±3.7	Apr. 9.8	
		3380-1	Evergreen, 320 m.	1	82	Apr. 5	
		4073	Mt. Hamilton, 650 m.	58	84.0±1.94	Apr. 22.7	
		*3966	Knights Ferry, 90 m.	57	67.4±1.92	Apr. 15.7	
		3383-11	Moccasin Creek, 275 m.	1	81	Apr. 4	
Central Valley (36° 40' N. lat.)	6n	*4074	Selma, 90 m.	60	126.3±2.59	June 5.8	none
		4152-11	Centerville, 115 m.	1	88	±May 15	
Central Sierra Nevada (39° 15' to 37° 49' N. lat.)	4n	3385	Grass Valley, 810 m.	5	67.2±2.47	Apr. 30.4	winter
		*3967	Groveland, 915 m.	32	83.4±2.19	May 13.8	none
		1315	Mather, slope, 1430 m.	5	94.0±1.69	May 14.0	
		*3778	Mather, meadow, 1400 m.	58	75.6±1.81	May 16.8	winter
		3968	Hetch Hetchy Rd., 1525 m.	61	71.0±1.71	May 22.6	
		*3969	Aspen Valley, 1950 m.	52	49.3±1.68	June 5.4	
		*3970	Yosemite Creek, 2200 m.	53	49.1±1.66	May 24.3	
		*3971	Tenaya Lake, 2500 m.	57	32.2±1.18	May 11.4	
		*3972	Tuolumne Mdws., 2620 m.	46	20.8±1.11	May 14.7	
		*3780	Slate Creek, 3050 m.	30	21.2±1.55	May 12.6	
		*3780	Big Horn Lake, 3350 m.	9	15.3±1.47	Apr. 29.6	
Mono Lake basin (38° N. lat.)	4n	*4075	Conway Summit, 2480 m.	17	27.6±2.23	May 25.6	winter
		*4076	Leevining, 2100 m.	55	43.5±1.64	May 22.1	
Northern California coast (39° 20' to 40° 50' N. lat.)	6n	3367	Fort Bragg, 25 m.	3	88.0±4.61	May 7.3	none
		3367-11	Cape Mendocino, 2 m.	1	50	May 1	
		3368	Clam Beach, 3 m.	4	100.0±1.45	May 3.0	

*Key races in the investigations.

TABLE 1—*Continued*

Geographical region	Ploidy		Number and origin	No. of plants	Longest stems (cm.)	First flowers	Dormancy
Northern California mountains (39° 45' to 41° 45' N. lat.)	6n	3376	SW. of Lane's, 60 m.	4	71.0 ±10.6	May 16.5	none
		4154	Van Duzen River, 825 m.	56	60.4 ±1.82	May 15.7	
		4155	Mad River Basin, 1220 m.	45	55.2 ±1.63	May 24.0	
		4156	Hayfork, 765 m.	47	73.5 ±1.39	May 19.9	
		4157	Douglas City, 1040 m.	57	69.8 ±1.14	May 16.2	
	4n	3375	Dyerville, 80 m.	5	113.0 ±9.74	May 3.8	none
		4158	S. of Dunsmuir, 530 m.	49	57.5 ±2.09	May 17.0	
		3374	Yreka, 800 m.	5	71.6 ±3.51	May 23.0	winter
		4159	Mineral, 1480 m.	28	48.8 ±2.68	May 23.6	
Oregon coast (42° 50' to 44° 40' N. lat.)	6n	3840-1	N. of North Bend, 30 m.	1	74	May 25	none
		3841-11	Yachats, 15 m.	3	37.3 ±7.64	May 16.6	
		3841-41	Newport, 30 m.	1	21	May 25	
		3841-51	Otter Crest, 60 m.	1	48	May 25	
	4n	3841-1	Port Orford, 20 m.	1	55	June 5	none
Oregon Coast Range (43° 5' to 44° 35' N. lat.)	4n	3369	E. of Myrtle Point, 90 m.	5	100.5 ±5.15	May 7.4	none
		3370	Camas Mtn., 440 m.	3	91.3 ±1.37	Apr. 29.7	
		3841-21	Alsea, 90 m.	2	49.5	May 1.0	
		3841-31	Alsea Mtn., 375 m.	3	64.0 ±2.51	Apr. 28.3	
		3841-61	Eddyville, 100 m.	1	56	±May 28	
		3841-71	Blodgett, 160 m.	1	93	±May 15	
		3841-81	Corvallis, 70 m.	2	76.0	±May 25	
Oregon Cascades (42° N. lat.)	4n	3373	Mt. Ashland, 2200 m.	4	23.0	June 2.5	winter
		3371	Gold Hill, 350 m.	3	105.6 ±3.33	May 11.0	none
		3372-1	E. of Prospect, 1400 m.	4	72.5 ±2.05	May 10.3	
Western Washington (46° 38' N. lat.)	6n	3837	Chehalis, 55 m.	2	96.0	May 27.5	none
Northern Great Basin (43° 40' to 42° 50' N. lat.)	4n	3372-11	Squaw Butte, Ore., 1500 m.	5	37.8 ±7.54	±May 25.0	winter
		3781	Hagerman, Ida., 1000 m.	48	60.1 ±1.72	May 24.8	
		3782	Pocatello, Ida., 1360 m.	34	56.6 ±1.63	May 29.4	
Aleutian Islands (52° N. lat.)	6n	4395	Kiska, 7 m.	59	20.0 ±1.00	Apr. 18.0	none
		4396	Kiska, 15 m.	60	23.6 ±0.60	Apr. 16.7	
		4397	Kiska, 150 m.	60	10.7 ±0.63	Apr. 17.3	winter
		4398	Kiska, 250 m.	49	8.8 ±0.62	Apr. 21.0	
		4399	Kiska, 300 m.	23	7.5 ±0.66	Apr. 14.3	
		4400	Kiska, 365 m.	31	8.1 ±0.69	Apr. 19.2	
Alaska coast (60° 8' N. lat.)	6n	2443	Seward, 12 m.	11	27.9 ±1.84	Apr. 28.8	winter
Northern Europe	6n	*2442	Denmark, coast, 3 m. (Skelskör, 55° 17')	11	42.1 ±2.28	May 15.4	none
		1808	Denmark, inland, 40 m. (Geel's Forest, 55° 49')	4	45.0 ±9.24	June 2.6	
		*3766	Swedish Lapland, 420 m. (Abisko, 68° 20')	55	27.8 ±1.83	Apr. 29.9	winter

*Key races in the investigations.
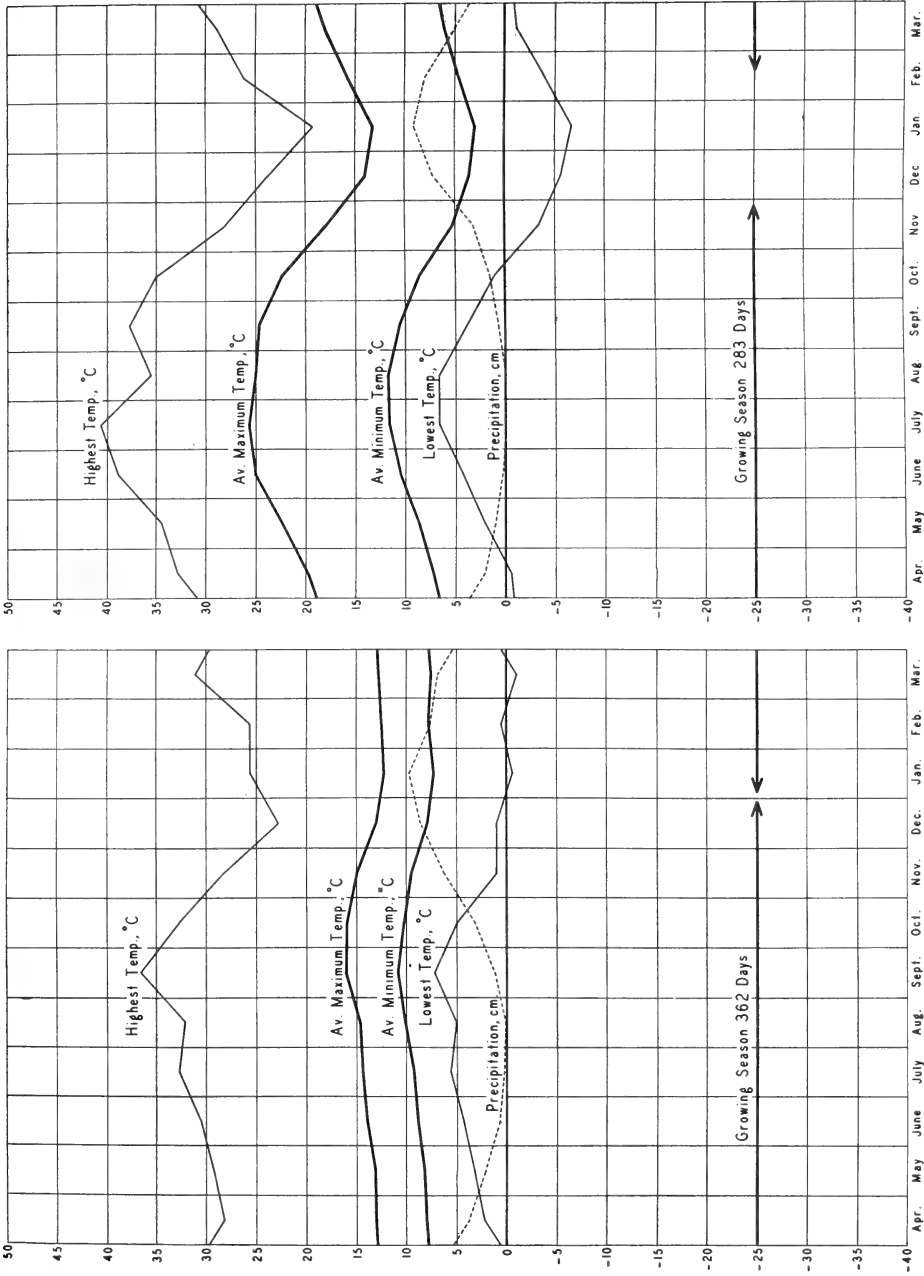
Fig. 2. Temperatures, precipitation, and average growing season (frost-free period) of a maritime station, Point Reyes, and of one between the Coast Ranges at Palo Alto. Based on United States Weather Bureau records for 39 years from Point Reyes, and 17 years from Palo Alto.

2

toward the coast, and the diurnal variations, especially during summer, are greater. The climate at Fresno, shown in figure 3, is typical of these conditions. Few cloudy days and the long growing season provide ideal growing conditions for irrigated crops in this important agricultural area. Much of the region is grassland with many ephemeral winter annuals and with more permanent vegetation along the watercourses and in the extensive alkaline flats.

At Groveland, Tuolumne County, in the Sierra Nevada at 862 m. elevation, summer and winter temperatures are below those of the San Joaquin Valley and the precipitation is much greater (fig. 3). This locality is on the lower border of the yellow pine belt in a forested region entirely unlike the Fresno grassland. In winter the average minimum temperatures at Groveland are at about the freezing point of water, and the growing season is shorter by more than 100 days than that at Fresno.

At successively higher altitudes in the Sierra Nevada, temperatures throughout the year are progressively lower. The amplitude of diurnal and seasonal variations is about the same, but winters become progressively longer and summers shorter. This trend can be seen by comparing the temperature curves for Groveland with those for Lake Eleanor at 1417 m. and Huntington Lake at 2134 m., presented in figure 4. At Ellery Lake, 2890 m., the highest station in the Sierras from which weather data are available, temperatures are lowest and growing seasons shortest (fig. 5).

In the Great Basin region east of the Sierran crest the climate is highly continental, with great variation in diurnal and seasonal temperatures and much lower precipitation. An example of this is shown in figure 5 by temperature and precipitation curves for Bridgeport, Mono County, at 1964 m. elevation. Comparison of these curves with those from Ellery Lake makes it evident that the climate at Bridgeport is more severe in some respects, although summers are warmer and growing seasons longer. Aridity and extreme temperature variations at Bridgeport give this climate a desert character that contrasts sharply with the equable maritime one of Point Reyes, only 200 miles farther west.

Three mountain ranges paralleling the coast line greatly influence the climates of the central California transect, for each range markedly decreases the coastal influence. Each rise in altitude brings a corresponding decrease in the temperature curves and to a certain degree increases the precipitation on the west side of the mountain. The decreased coastal influence is felt more during the summer, when trade winds from the hot, dry interior prevail, than during the winter months, when antitrades blow in from the sea.

FRESNO, CALIF. (ELEV. 100 M.)
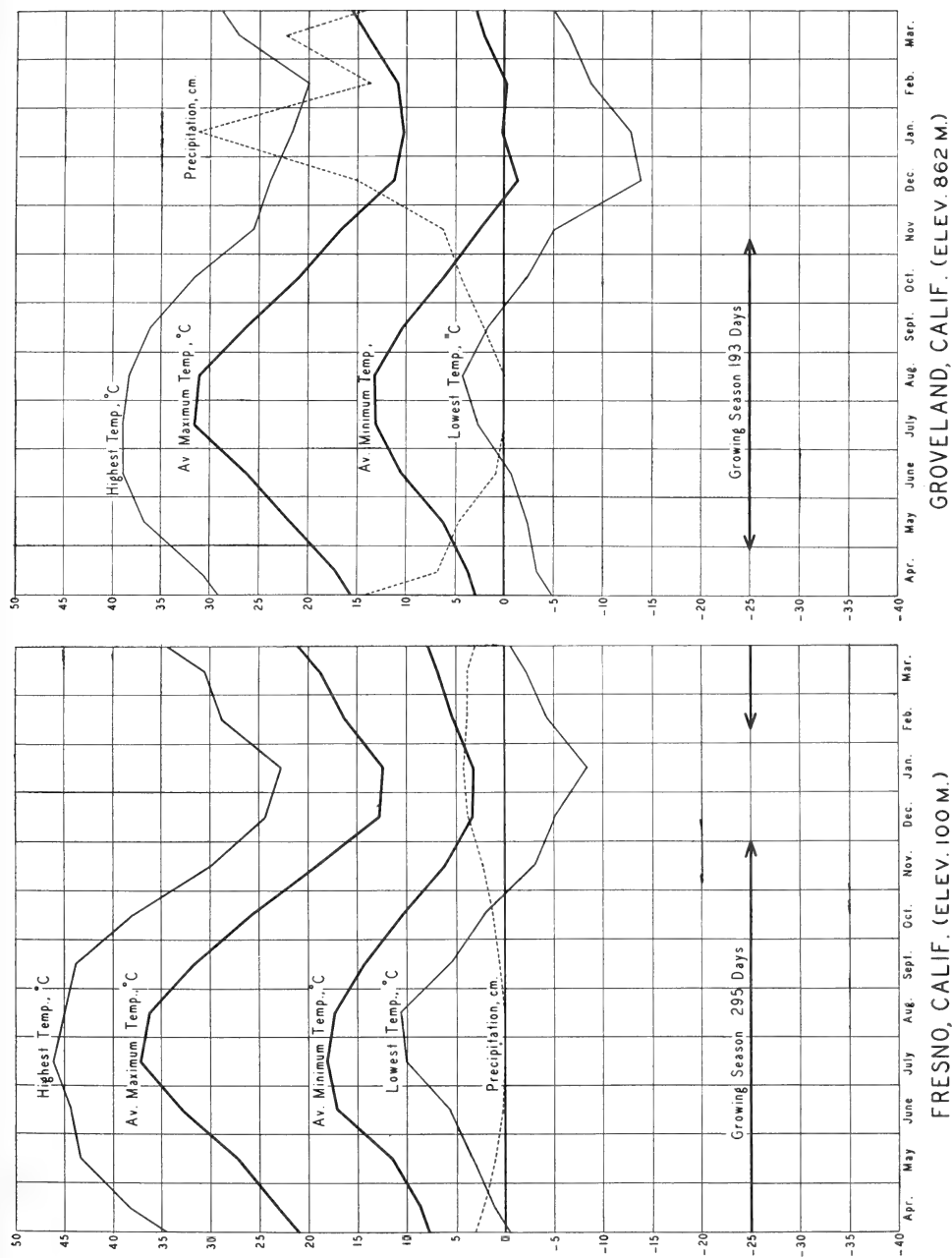
GROVELAND, CALIF. (ELEV. 862 M.)

FIG. 3. Temperatures, precipitation, and average growing season (frost-free period) of Fresno, in the San Joaquin Valley, and of Groveland, in the lower Sierra Nevada. Based on United States Weather Bureau records for 42 years from Fresno, and 7 years from Groveland.

Fig. 4. Temperatures, precipitation, and average growing season (frost-free period) of Lake Eleanor, at a mid altitude in the Sierra Nevada, and of Huntington Lake, at a higher elevation. Based on United States Weather Bureau records for 31 years from Lake Eleanor, and 24 years from Huntington Lake.
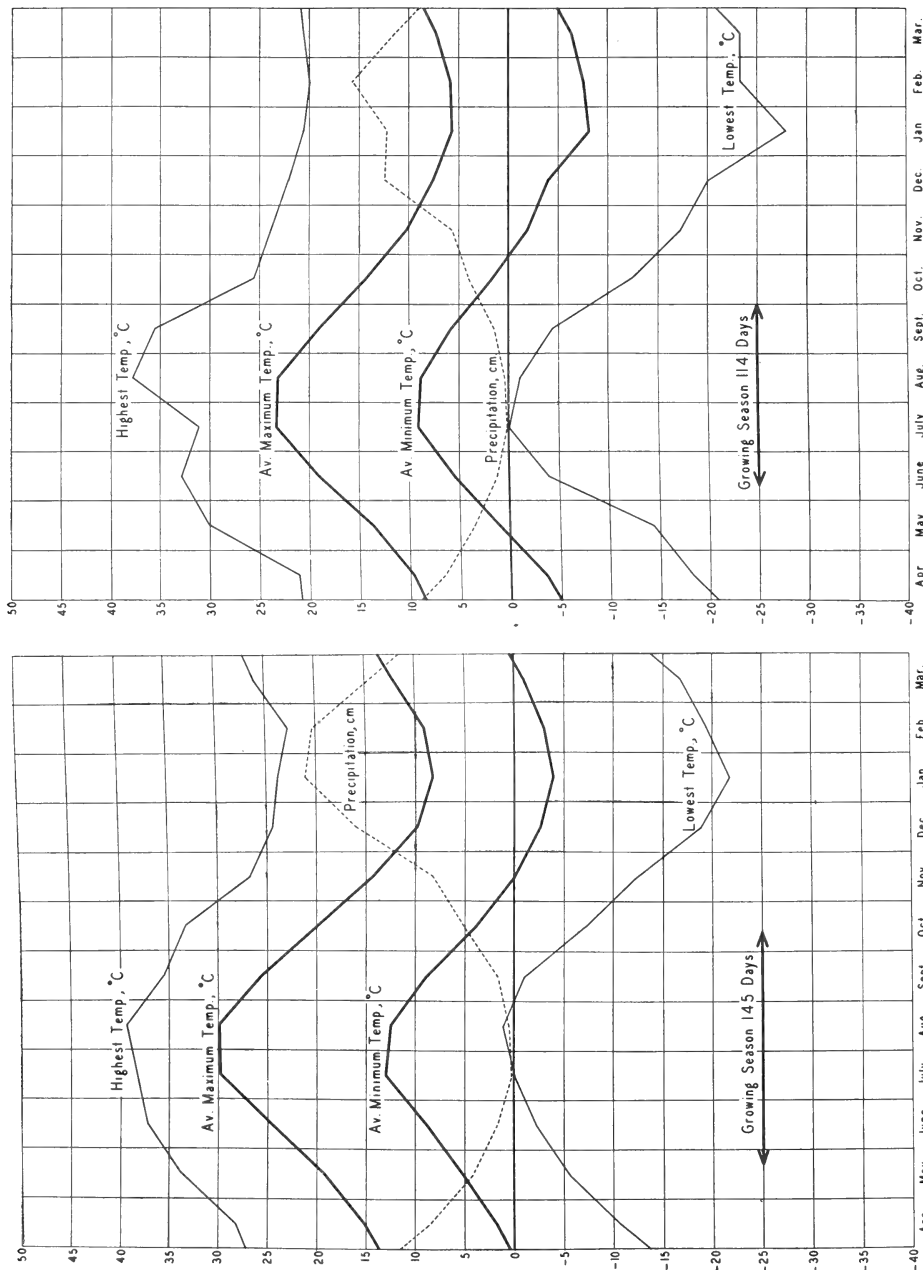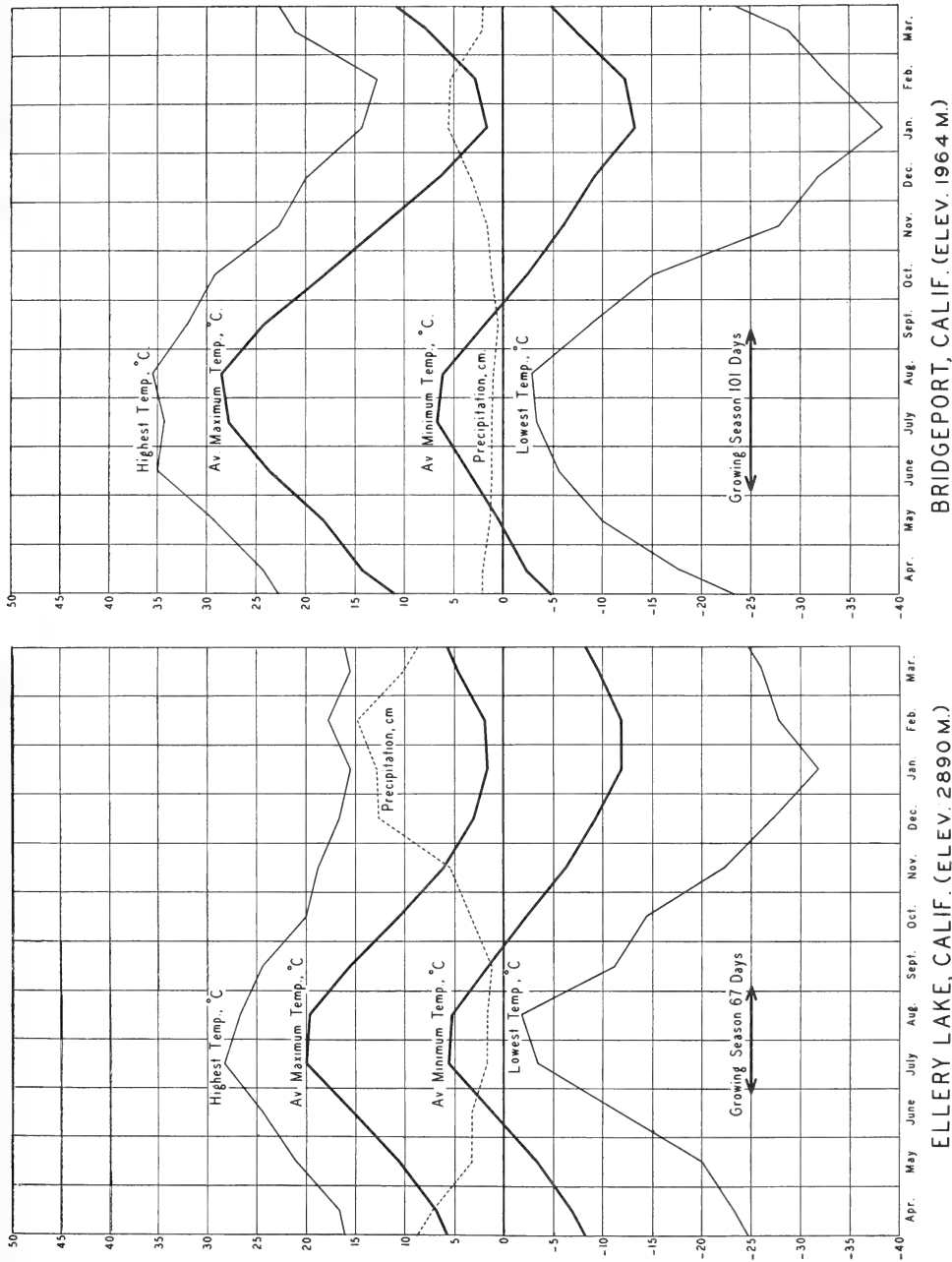
FIG. 5. Temperatures, precipitation, and average growing season (frost-free period) of Ellery Lake, near the crest of the Sierra Nevada, and of Bridgeport, on the Great Basin Plateau. Based on United States Weather Bureau records for 16 years from Ellery Lake, and 12 years from Bridgeport.

The various races of *Achillea* depicted in figure 1 reflect their native climates. The plant and the climate are inseparable, and in the following account the one will frequently be linked to the other.

THE BODEGA AND SAN GREGORIO POPULATIONS

Along a narrow coastal strip extending from Alaska to San Luis Obispo County, California, grows a maritime form of *Achillea* characterized by a compact habit, short, thick stems with crowded internodes, broad, flat-topped inflorescences, and large, thick leaves with crowded, overlapping segments. This form is of relatively rare occurrence, for it is confined to the more exposed bluffs and slopes that receive the full sweep of the spray-laden winds. Culture 3776, from the Bodega coast 2 miles north of Salmon Creek, Sonoma County, California, has been studied in detail as a representative of this readily distinguishable maritime race.

At places only slightly protected from severe ocean winds the maritime race is replaced by taller forms that are genetically distinct but physiologically rather similar. They constitute a race that is common on the seaward side of the outer Coast Ranges of central California, and that differs from the maritime race mainly in greater height and longer, more openly segmented leaves. A population from just south of San Gregorio, San Mateo County, on the San Francisco peninsula, has been studied in detail as a representative of the coastal race from less exposed habitats. It was collected on a grassy slope about one mile from the ocean.

INDIVIDUAL VARIATION. Two characteristics stand out in the *Achillea* populations studied. One is the inherent variability observed within each, and the other is the relative distinctness of almost every population despite its variability. This is clearly shown in figure 6, which compares samples of 7 plants each from the Bodega and San Gregorio populations. Within each population the plants differed in height, size, leaf texture, mode of branching, size and shape of ray florets, number of florets per head, degree and time of flowering, and other characters. The relative importance of the extremes is overemphasized in figure 6; actually there is a preponderance of intermediate classes. As an indication of genetic potentialities within natural populations, however, the presence of extreme variants is important.

The frequency graphs in figure 1 indicate the extent of variation within each of these coastal populations, and figure 6 aids in visualizing the differences. The frequency curve for the Bodega race comes to a steeper peak at the mean value than does that for the San Gregorio race, showing
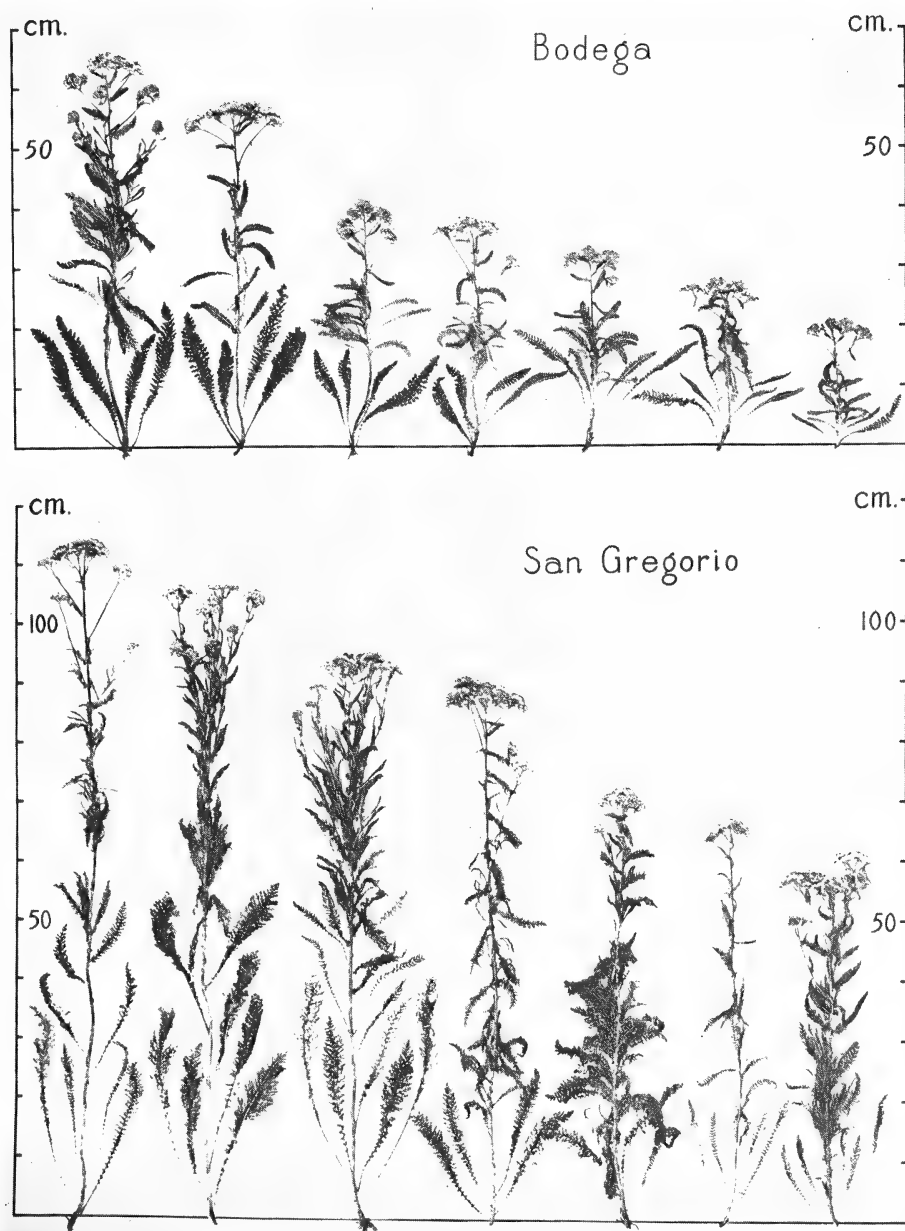
FIG. 6. Comparison of individual variation among plants of the maritime Bodega population with that in the taller coastal San Gregorio population, as shown by specimens taken in June 1941 from a uniform garden at Stanford.

Left to right, the plants are as follows: Bodega, 3776-3, -4, -27, -18, -25, -28, -29 (cf. table 5); San Gregorio, 3777-1, -5, -26, -7, -28, -27, -30 (cf. table 6).

that the former has a greater preponderance of individuals in the middle classes. From the extreme wind-swept maritime environment at Bodega a more rigorous selection might be expected than from the less specialized environment at San Gregorio. The total range of variation, however, is as great in the Bodega population as in the San Gregorio.

These two populations are among the most contrasting from the seaward side of the outer Coast Ranges, but even they show overlapping variation, as is evident in figure 6. The tallest plants of the dwarf Bodega population exceed the shortest of the taller San Gregorio. Some plants from San Gregorio have the crowded leaf segments typical of plants from Bodega. This and other recombinations of characters suggest that genes may have been exchanged between these races.

Gene exchange between natural populations is even more evident in protected areas close to the sea where dwarf maritimes have combined with taller, more inland plants. For example, in a swale at the base of Montara Mountain, near the sea, short and tall plants grow together. Cultures 3771 and 3772, listed in table 1, are the offspring of two of the tallest plants found there; cultures 3769 and 3770, of two of the shortest. The progenies from the tall plants are significantly taller than those from the short ones despite the fact that these Achilleas are obligate cross-pollinators. Furthermore, the progenies of the shortest plants do not differ significantly in height from culture 3768, collected from the exposed coast about one-half mile to the west. From such variable populations it should be possible, through selection, to derive forms that differ materially, as has already been pointed out (Hiesey, Clausen, and Keck, 1942).

SEASONAL CHARACTERISTICS. One of the most important differences between the climatic races of *Achillea* is that in seasonal periodicity. This character is intimately associated with climate and reveals some of the physiological differences between the races.

The climate from which the Bodega race came is much like that of near-by Point Reyes, whose temperature and precipitation curves are shown in figure 2. The climate at San Gregorio is rather similar but less windy. In this mild coastal climate the most active period of growth for *Achillea* is during the winter, when rains reach their peak. In the Stanford garden both races are essentially evergreen, and most active during the moist winter period, when the days are short and the nights rather cold. Large rosettes of leaves unfold, unchecked by the frequent frosts, until April, when stocky flowering stems begin to develop. The stems of the tall San Gregorio population elongate more rapidly than those of the

Bodega, and flower two weeks earlier (table 1). As the stems mature, the rosettes become less active, but this is not noticeable at first in the Bodega race, which, in early June, forms attractive green clumps topped with white inflorescences, as illustrated to the left in figure 8 (p. 33).

Flowering continues for more than a month as successive stems on each plant mature. Different individuals vary considerably in time of flowering, extending the blooming season so that in the Bodega population open flowers may be found throughout July. A month later the seed has ripened and the stems have turned brown, but the rosettes remain green throughout the year. The Bodega and San Gregorio populations, in common with others from the coast, flower freely at Stanford, each individual producing an abundance of stems. Seedlings develop inflorescences within nine months after sowing, but full maturity and maximum size are not attained before the second year. Survival is excellent, but, as in all Achilleas, vigor deteriorates after several years' growth in one place unless renewed by transplanting.

The climate at Stanford during the summer and fall is too dry for plants of the coastal races to grow successfully without irrigation. Forms native at Stanford become dormant during this dry season and are referable to the race of the dry interior foothills described below.

THE CLAYTON AND KNIGHTS FERRY POPULATIONS

As one passes from the coastal belt of central California to the interior valleys and slopes, the climate becomes more arid, and diurnal and seasonal amplitudes of temperature are greater. This trend toward colder winters, warmer summers, and reduced rainfall is already evident at Stanford in the Santa Clara Valley and becomes more pronounced east of the inner Coast Ranges on the foothill slopes facing both sides of the San Joaquin and Sacramento valleys.

In these more arid regions is another kind of race, exemplified by the populations from near Clayton, Contra Costa County, and Knights Ferry, Stanislaus County. Both these populations are from the oak-grassland savannas of the interior foothill regions. The Clayton population originated in the foothills east of Mount Diablo, 11 miles east of Clayton on the road to Byron, and the Knights Ferry population in the bluffs above Wildcat Creek at its junction with the Stanislaus River west of Knights Ferry.

SEASONAL PERIODICITY. Like the coastal races, the Clayton and Knights Ferry cultures make their principal growth during the winter and early

spring season, when they use the small amount of rainfall that is available in their natural habitats. Their growing season is much shorter than that of the coastal forms. They flower and ripen their seed earlier, so that by the time the winter supply of moisture is exhausted, in May or June, they have completed their seasonal growth and pass into a period of dormancy. At this time the stems and leaves dry up, and the living underground parts remain inactive in the warm, dust-dry soil. With the recurrence of lower temperatures and winter rains, the plants spring into rapid growth to repeat their ephemeral, drought-escaping cycle,

Morphologically, these interior forms differ from the coastal in their grayer, more pubescent herbage, their thinner, scantier leaves and stems, and their generally smaller inflorescences and reduced bulk. Two physiological differences stand out in the garden at Stanford: the interior forms flower approximately one month earlier than the coastal populations, and they do not become active in the dry season when irrigated. The differences in the reactions of the coastal and interior foothill races stand out even more clearly at the mountain stations, as will be seen in chapter III.

INDIVIDUAL VARIATION. In the garden at Stanford the foothill populations showed considerable variability. This is indicated in part by the frequency graphs in figure 1, showing variation in height, but other characters, such as size and texture of leaves, size of heads, branching, length of rays, and amount of pubescence, were also variable. Earliness and summer dormancy of the populations from Clayton and Knights Ferry are relatively uniform.

There is no clear-cut distinction between the typically coastal and the interior foothill types. The many climatic niches afforded by the complex topography of the Coast Ranges have doubtless resulted in the selection of a correspondingly varied series of populations with extensive opportunities for recombining. The distinctions between the short maritime, the tall coastal, and the interior foothill races are nevertheless genetic and reflect the constantly sifting action of natural selection.

THE SELMA POPULATION

The San Joaquin Valley of California is a physiographic area that differs markedly in climate, geological history, and vegetation from the coastal regions to the west and the Sierra Nevada to the east. It is a broad, arid plain, highly fertile in those vast tracts that are irrigated by the channeled waters of the Sierran rivers flowing into it.

The climate of this area is described by the graph for Fresno in figure 3,

which can be compared with similar graphs for other localities. Fresno differs from Palo Alto and Stanford, for example, in its higher maximum summer temperatures, much greater diurnal variation in temperature, and reduced precipitation, yet the total length of its growing season, as measured by the average frost-free period, is about the same.

A distinctive giant and gray-pubescent race of *Achillea* grows in the sandy bottom lands of the valley in Fresno County at a number of places between Fresno and Selma, and near Centerville. This is the form described as *A. gigantea* Poll. Under the intensive cultivation now practiced in the region, this *Achillea* is confined to waste places such as grassy stretches along roadside ditches and near the edges of tule ponds that mark the termini of streamlets issuing from the Kings River basin. In springtime it is often found growing in shallow water. This race utilizes the long growing season, intense insolation, and warm temperatures of its environment for the vigorous synthesis of the materials used in building its towering stems. The Selma population used in these investigations grew along the edges of Rockwell Pond, 4 miles northwest of Selma, where plants 2 m. high were found. This tule pond is on the valley floor well outside the foothill oak belt.

The Selma form differs markedly from the neighboring foothill race in its developmental characteristics. It is unlike other Achilleas in that the stems begin to elongate early, the rosette is never strongly developed, and the plant depends mainly on its cauline leaves. At Stanford, the tall, robust stems grow very slowly during the coolest part of spring, when the coastal and foothill races are active, but develop more rapidly as the weather becomes warm in summer, when the coastal races have slowed down their growth and the foothill forms are dormant. It flowers longer than any other race, beginning in June and continuing until mid-August, and, when provided with adequate moisture, attains a size nearly as great as it would in its native habitat. It is less active in fall and winter than the preceding races, but new branchlets, developing in the lower axils of the old stems, keep the plant green until new stems develop from the rhizomes in March.

The individuals of the Selma form vary in height to a greater degree than any of the other populations, as can be seen from the frequency diagram in figure 1. They vary also in details of branching and density of pubescence, but as a whole have several distinctive qualities that set them apart from the other races already discussed. Morphologically this race appears to be most closely related to the interior foothill forms represented by the Clayton and Knights Ferry cultures. Since these come from

near by, it is possible that they and the Selma race stem from the same ancestral stock. Each would seem to be the natural result of continuous selection.

Unfortunately, it was not possible to test the Selma race in the gardens at Mather and Timberline because of transportation restrictions brought on by the war. Results from experiments under controlled greenhouse conditions, however, reported in chapter IV, show differences in temperature requirements for growth of the Selma and coastal races.

THE GROVELAND POPULATION

In passing from the area of the arid interior foothill type, represented by the Knights Ferry population at 90 m. elevation, to Groveland at 915 m., one enters a very different vegetational zone. Knights Ferry is in semi-arid grassland with scattered trees of *Pinus Sabiniana, Quercus Douglasii,* and *Aesculus californica.* Groveland, on the other hand, lies well within the lower edge of the coniferous forest covering the Sierra Nevada, which here consists chiefly of *Pinus ponderosa, P. Lambertiana, Libocedrus decurrens,* and the deciduous broad-leaved *Quercus Kelloggii.* Since the temperatures are lower and snowfalls occur at Groveland, most species are forced into dormancy during the winter season. In this region the tetraploid *Achillea lanulosa* has replaced the hexaploid *A. borealis* of the foothills and Coast Ranges.

Some of the essential features of the climate at Groveland are described by the weather graphs in figure 3. The average minimum winter temperatures drop to or below freezing, a critical temperature that accounts for the presence of snow, which is not found at the localities at lower altitudes, such as Knights Ferry and Selma.

The Groveland population used in the present experiments grew in a dryish meadow in the coniferous forest 6 miles east of Groveland, near the Tuolumne Ranger Station. It is the tallest of the Sierran races at Stanford, and marks the beginning of a series of successively shorter-stemmed forms found at increasing altitudes, as illustrated in figure 1. As compared with populations from the foothills and the coast, this form has slender stems and small ray florets, but there are no pronounced morphological characters by which it can be distinguished from the hexaploids of the Coast Ranges and foothills.

In the garden at Stanford, the Groveland form differs considerably in its seasonal reactions from the Knights Ferry and Clayton strains of the interior foothills, but is similar to the forms from the coast. It is active during the winter and spring months, and flowers in May at about the

same time as the coastal races, but one month later than the neighboring foothill race. It remains semiactive during the summer and fall. Its winter activity is not quite so pronounced as is that of the coastal races.

A principal difference between the Groveland population and those from the coast and the foothills is a physiological one, which becomes evident when the forms are compared at the mountain stations. There the ambiguous similarity between them, so noticeable at Stanford, disappears, as will be seen in chapter III. In many respects the Groveland form is pivotal, having qualities common to the coastal and the higher montane races.

This form shows quite marked individual differences. A fuller treatment of the variation will be found under the description of the Mather form, since the comparative composition of these two populations is of critical interest in the study of variation in *Achillea* on the western slope of the Sierra Nevada.

THE MATHER POPULATION

Mather is in the center of the coniferous belt of the Sierra Nevada, where timber reaches its maximum size. Here, at 1400 m. elevation, the temperatures are somewhat lower than at Groveland at 915 m., showing an average difference of 1.8° C. The general amplitude of variation between winter and summer temperatures is about the same, as can be seen by comparing the weather graphs for Groveland and Lake Eleanor (essentially the equivalent of Mather) in figures 3 and 4.

The races of *Achillea* from the Mather and Groveland environments show important differences, but the picture is complicated by the overlapping variation observed in the population samples. From a study of such populations it is possible to gain a view of the screening processes that operate in natural selection.

SEASONAL PERIODICITY. The Mather populations used in the present study grew in the large, open meadow in which the transplant garden is located. This meadow is surrounded by slopes forested with tall *Pinus ponderosa* and *Libocedrus decurrens*. The Mather meadow form is for the most part dormant during the winter months at Stanford, but some individuals, like those from Groveland, remain green and moderately active. Those that are winter-dormant show signs of new growth early in March, and all flower, on the average, a few days later than those from Groveland. The Mather plants remain active throughout the summer—and, to a lesser extent, autumn—but become dormant in January, when

temperatures drop below freezing. They require more time to reach maturity than do plants of the coastal, foothill, and Groveland populations. At Stanford the Groveland plants flower the first year, but most of the Mather Achilleas, like those from Aspen Valley and higher altitudes, require a second year to attain this stage of development.

Achillea also grows on the pine-covered slopes at Mather, in a considerably drier environment than that of the meadow plants just discussed. A sample of 5 individuals from these drier slopes (culture 1315 of table 1 and of the 1940 publication) is consistently winter-active at Stanford, as are those from Groveland, and is considerably taller than those from the meadow. This limited evidence suggests that the drier, warmer hillsides may be populated principally by plants of the winter-active type similar to those of the Groveland form, and the meadows by plants predominantly of the winter-dormant type similar to those from higher altitudes. This situation appears to parallel that in *Potentilla glandulosa* at Mather, in which there are clear-cut differences between the moist meadow and dry slope ecotypes, as reported earlier by the writers (1940).

INDIVIDUAL VARIATION. Small but statistically significant differences between the Mather meadow and the Groveland populations are found in morphological characters such as stem height when the two are compared in the garden at Stanford, as may be seen in figure 1 and table 1. Individual variation within each population, however, obscures these small differences. That variation extends to physiological characters such as winter dormancy at Stanford is clear from the preceding paragraphs. Similar variation was observed in a population of 61 individuals originally from a meadow some 6 miles from Mather and 125 m. higher in elevation (culture 3968 of table 1). Leaf, stem, and flower characters of the Mather population vary from the Groveland type, on the one hand, to the Aspen Valley, on the other. Yet statistically the three populations are significantly distinct. This is much more clearly seen when their responses are compared at the three transplant stations, as will be evident in the following chapter.

THE ASPEN VALLEY POPULATION

The climate at Aspen Valley, at 1950 m. elevation, is definitely cooler in summer and winter than that at Mather, and the growing season is shorter. This locality is also in a heavily timbered belt, but the composition of the forest changes, *Pinus Jeffreyi* replacing *P. ponderosa, Libo-*

cedrus becoming rare and *Abies concolor* more frequent, with *Pinus Murrayana, Abies magnifica,* and *Populus tremuloides* appearing as new components. A comparison of the weather graphs for Lake Eleanor and Huntington Lake, in figure 4, shows approximately the differences in climate between Mather and Aspen Valley. Huntington Lake is 175 m. higher than Aspen Valley but farther south, so the general characters of the two climates are probably similar.

The Aspen Valley population grew in a small meadow along the Tioga road 1 mile beyond Aspen Valley Lodge. The Achilleas from this area are shorter-stemmed than the Mather form, as can be seen in figure 1. The generally shorter leaves and smaller rosettes are also obvious, but as will be seen in chapter III the differences between the Aspen Valley and Mather races are accentuated more in the garden at Stanford than at Mather.

At Stanford the Aspen Valley population is strictly winter-dormant, presenting a distinctly different picture from the Groveland and lowland races. In its native habitat, where the winter is severe, it is inactive for at least half the year, but at Stanford the dormancy lasts only two or three months. By the middle of March its new growth commences, and by late May some of the plants have begun to flower, but at that time individual variability in earliness and capacity to flower at Stanford makes the culture very uneven. Later plants may not develop mature stems before the middle of summer, and a proportion may remain rosettes throughout the year. It flowers three weeks later than the Mather forms at Stanford, where it is the last of the Sierran populations to flower (table 1). When compared with the earlier-flowering races from higher altitudes, this population shows a relatively slow development.

The variability within the Aspen Valley population is probably no greater than in most of the others, but at Stanford it appears especially impressive because of the combination of differences in form, earliness, and seasonal development. Individual variation ranges from plants like some found at Mather to those like some found at Yosemite Creek, 250 m. higher in elevation.

THE YOSEMITE CREEK POPULATION

The forest at Yosemite Creek, at 2200 m. elevation, is thinner and of somewhat different composition from the one at Aspen Valley. The red fir (*Abies magnifica*) largely takes the place of the white fir (*A. concolor*), and, with *Pinus Murrayana,* becomes the predominating tree of

the forest, although Jeffrey pine still occurs frequently. Bare expanses of granite appear here and there, but the pockets of soil are fertile and the crevices are filled with herbaceous species that even on sunny slopes find adequate moisture left by late-melting snows. The growing season becomes progressively shorter toward the mountaintop.

The seeds for the Yosemite Creek population were collected from a small colony growing in a dry creek bed in the dense shade of *Pinus Murrayana* near the road crossing at Yosemite Creek.

At Stanford this population resembles the one from Aspen Valley, but tends to flower more freely and two weeks earlier. It is more variable, consisting of plants ranging from tall, luxuriant forms with large, green, sparsely pubescent leaves to rather dwarf types with small, narrow, gray-canescent leaves similar to those of plants from alpine environments. The range of variation is illustrated in figure 7, showing herbarium specimens of 7 plants of the Yosemite Creek form grown at Stanford compared with a corresponding sample of the Tenaya Lake form, from 300 m. higher in elevation. The figure shows clearly that the variations of the two populations overlap. The Tenaya Lake material is of the subalpine (*alpicola*) type, with preponderantly gray-canescent narrow leaves and short, slender stems. The transplant results reported in chapter III indicate, however, that the Yosemite Creek population is physiologically more uniform than its morphological variability would seem to indicate.

Although the winter dormancy of the Yosemite Creek population at Stanford is as prolonged as that of the Aspen Valley form, the former type develops more rapidly and therefore flowers earlier. A slow but fairly active growth continues in the rosettes throughout summer and fall.

THE TENAYA LAKE POPULATION

At Tenaya Lake the vegetation assumes a subalpine aspect, which is accentuated by the massive glaciated domes of bare granite that tower above it. In the crevices of these cling venerable specimens of *Juniperus occidentalis*. *Pinus Murrayana* is the common tree in the forest, but interspersed are also stands of *Abies magnifica* and *Pinus monticola*. Many typical alpine species are found in the herbaceous flora. Weather data are lacking from a site that corresponds to Tenaya Lake at 2500 m. elevation, but the climate can reasonably be assumed to be intermediate between that of Huntington Lake at 2134 m., graphed in figure 4, and that of Ellery Lake at 2980 m., in figure 5.

The *Achillea* sample used in this study came from the slopes above the northern shore of the lake. Between Yosemite Creek and this point a

readily perceptible morphological change takes place in the Sierran Achilleas, for below are the forms with the large, wide, green leaves of *lanulosa typica,* and above are those with the less compound, short, nar-
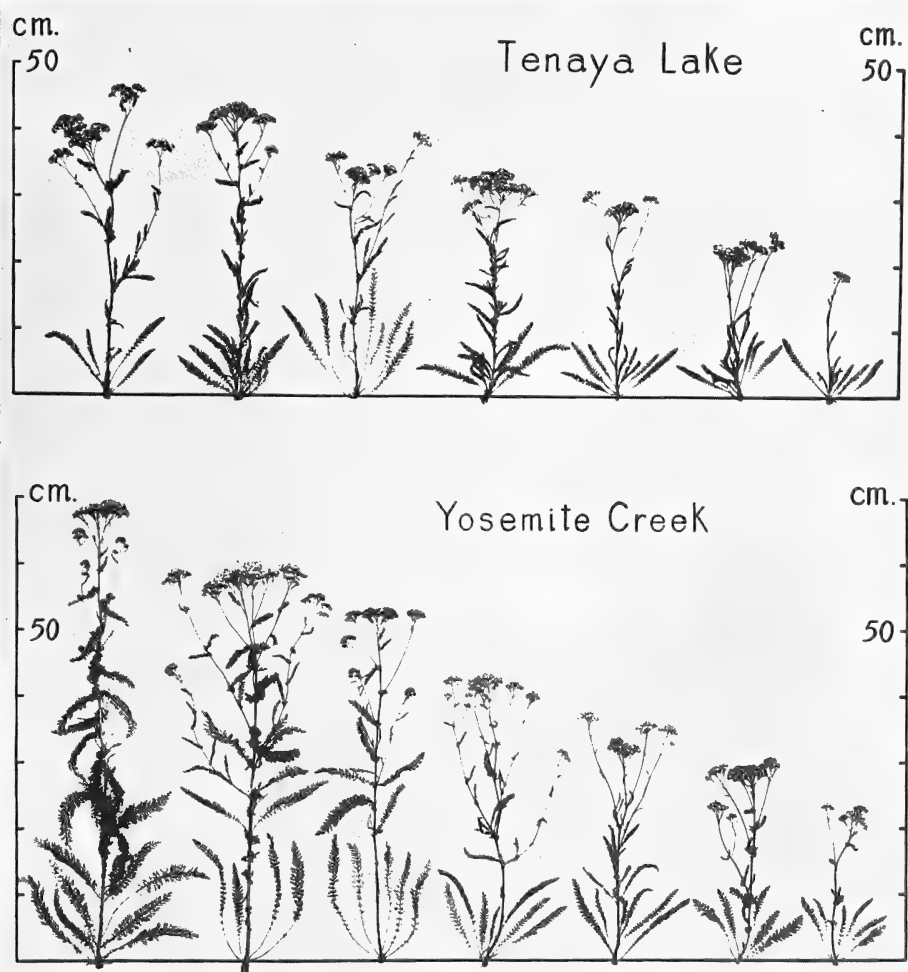
FIG. 7. Comparison of individual variation among plants of a high-Sierran population, Tenaya Lake, at 2500 m., with that in one from a lower altitude, Yosemite Creek, at 2200 m., as shown by specimens taken in June 1942 from a uniform garden at Stanford.

Left to right, the plants are as follows: Tenaya Lake, 3971-26, -5, -25, -11, -20, -16, -21 (cf. table 13); Yosemite Creek, 3970-6, -3, -18, -9, -12, -13, -30 (cf. table 12).

row, usually gray-canescent leaves of *lanulosa alpicola.* This change is quite obvious in figure 1, but a few plants of *alpicola* morphology were present in the Yosemite Creek population. The Tenaya Lake plants have the qualities of a subalpine form both in general appearance and in their

3

seasonal reactions at the three transplant stations. Since the plants are smaller than those of races from lower elevations, individual differences do not stand out so clearly although the relative magnitude of the variation is similar. This point is illustrated in figure 7.

In the Stanford garden the Tenaya Lake form flowers earlier and is shorter than the Yosemite Creek form, as is evident from table 1 and figures 1 and 7. The two show an even sharper contrast at Mather, where the Yosemite Creek form develops vigorously and the Tenaya Lake weakly, with shorter stems and less ability to flower. At Timberline the Tenaya Lake is one of the most vigorous populations in the climatic series.

THE TUOLUMNE MEADOWS POPULATION

In the subalpine meadows of the Sierra Nevada, *Achillea* is rather abundant in the open and in the partial shade of *Pinus Murrayana*. The seeds grown were collected on the western edge of Tuolumne Meadows at 2620 m. altitude. At all the transplant stations this population shows much the same characteristics as do the others from Tenaya Lake and upward. The characters that are common to all these forms are short stems, short-branched inflorescences, and narrow, more or less gray-pubescent leaves. At Stanford, however, the material from Tuolumne Meadows is significantly shorter-stemmed than that from Tenaya Lake, and at the mountain stations also it shows differences in earliness and frost resistance.

The Tuolumne Meadows population has a long period of winter dormancy at Stanford. With the beginning of spring growth the plants have weak rosettes and a generally starved appearance which is probably due to the active respiration of stored food materials during the relatively warm winter. As new leaves unfold and active photosynthesis begins, the plants regain their vigor. Like others from high altitudes, this form flowers very erratically, the first flowers appearing between April 22 and July 2, with some plants failing to flower at all. Flowering stems produced later in the season are taller and more vigorous than those developed on the same plant earlier. The erratic flowering of many high-altitude plants at Stanford can probably be associated with their general depletion during the mild winters.

The population from Tuolumne Meadows is a variable one. Although typical Achilleas from such high altitudes have gray-canescent leaves, about one-third of the Tuolumne Meadows individuals have greenish leaves like plants from lower elevations. These plants are alpine in other char-

acters, however, having short, slender stems and small leaves. Conspicuous variation in the length and width of ray florets and in the number of disk florets per head also occurs, producing rather striking differences in the showiness of individual plants. Variation in floral characters occurs in most of the populations from any altitude, but the Tuolumne Meadows population shows somewhat greater variation than the others. The usual diversities in height, vigor, and earliness observed in other populations are also features of this one.

Though its variation is conspicuous, the Tuolumne Meadows population bears the stamp of high-altitude material only. It does not include any individual that matches an Aspen Valley plant, for example, though a few could be mistaken for Yosemite Creek variants.

THE TIMBERLINE POPULATION

This population came from 3050 m. elevation in Slate Creek Valley, Mono County, east of the Sierran crest, the peaks of which rise to 3900 m. This location is within the Harvey Monroe Hall Natural Area, near the upper limit for trees, at the site of the Timberline Transplant Station. A migration route over the divide is afforded by near-by Tioga Pass, at the same elevation as the transplant station. The Achilleas that furnished seed for this experiment grew principally on south-facing rocky, sunny slopes above the gardens in scattered timber of *Pinus Murrayana* interspersed with occasional individuals of *P. albicaulis*. Deep snows occur in winter and often linger in a corner of the garden until early July, and even later on adjacent shaded slopes. Most of the herbaceous vegetation is forced into dormancy for at least nine months of the year. The weather graph in figure 5 for Ellery Lake, 3 miles away, gives approximate values for temperature and precipitation in this vicinity, although, as explained on page 46, the conditions at Timberline are more severe than at Ellery Lake.

The seasonal reactions described for the Tenaya Lake and the Tuolumne Meadows populations are equally characteristic of the Timberline population. It appears that the main difference among the three is that the Tenaya Lake population is slightly better able to take advantage of the longer growing season at Stanford. As will be seen in chapter III, there are some differences in reactions among the three populations at the transplant stations that may point to significant ecological differences.

In the Stanford garden the Timberline population shows as great individual variation in all the usual characters as do populations from lower

altitudes. When the variations within the Tenaya Lake and Tuolumne Meadows populations are considered, there seem to be no truly significant differences between these forms. The means are distinct for some characters under some sets of conditions, but it is difficult to prove that the differences are greater than might be expected of random samplings from different populations growing in the same climatic region. From the present data, these seem to be small genetic differences that possibly are of selective value in high-altitude habitats. The sampling is inadequate to answer this question conclusively.

THE BIG HORN LAKE POPULATION

This form, representing the most extreme alpine of the series, comes from the highest elevation at which the species has been found on the transect. Its native habitat is a lake shore in a glacial cirque on the north face of White Mountain, Mono County, at 3350 m. altitude, which is within the Harvey Monroe Hall Natural Area only 1.5 miles southwest of the habitat of the Timberline population. A perennial snow field lies on a north-facing slope above the lake, and an active glacier is carried at the same elevation on the adjacent Mount Conness. Gnarled mats of *Pinus albicaulis* 1 m. high form small patches of elfinwood at this uppermost fringe of the timber belt. Although weather records are not available, it is certain that conditions at Big Horn Lake are much more extreme than at Ellery Lake, 460 m. lower in elevation, weather records for which are shown in figure 5.

The individuals used in the experiments were transplants in flower dug September 13, 1941, from ten different colonies near the lake shore. No seeds were ripe when the collection was made, although freezing weather had already set in and native Achilleas near Timberline station carried ripe seed. Only in exceptional years with growing seasons much longer than usual are Achilleas at Big Horn Lake able to attain full maturity.

This is the dwarfest of all the Sierran populations of *Achillea*. At Stanford it survives but is not very floriferous. It resembles the other high-altitude forms in having small leaves and gray canescence, but is shorter-stemmed and comes to flower an average of two weeks earlier than the Timberline form, as is shown in table 1. This difference is statistically significant. The Big Horn Lake plants have a relatively long winter dormancy at Stanford, but some individuals spring into early flower as soon as the weather becomes warm in April, showing the same speedy development as under alpine conditions. In many individuals, however,

the early spring growth is vegetative and meager, reflecting a depletion of food reserves during the relatively warm winter, as was described for the populations from Tuolumne Meadows and Timberline. In all three forms a second crop of stems often overtakes the first as growth progresses during the season, but the dwarfer character of the Big Horn Lake plant is always retained.

Even this small alpine population is variable, although probably to a lesser degree than the Timberline one. Despite the small sample, consistent individual differences in height and earliness appeared in all three gardens. In the population from Timberline there are dwarf, early-maturing individuals of a type similar to those found at Big Horn Lake, suggesting a source of variation from which this extreme alpine could have arisen through selection.

THE CONWAY SUMMIT POPULATION

In the region of the transect across central California the eastern escarpment of the Sierra Nevada rises very abruptly about 1800 m. from the floor of the Great Basin plateau. This flank of the range is distinctly more arid than the western slope, but is watered by short snow-fed streams that pour into saline sinks such as Mono Lake. The *Achillea* at Conway Summit, halfway down the escarpment at 2480 m. altitude, is distinct from the subalpine forms found at Tuolumne Meadows and Timberline, and the alpine from Big Horn Lake. It occurs along a moist streamway, with grasses and mesophytic herbs and extensive stands of *Artemisia tridentata,* the ubiquitous sagebrush of the Great Basin, only a few feet away. The greener herbage, larger basal leaves, and taller stems distinguish the Conway Summit from the alpine and subalpine types just discussed.

The usual amount of individual variability is found in this population. Heights and leaf sizes overlap those in the Leevining material from a lower elevation. There are no plants that match those from the alpine environments, nor are there any very similar to plants from Tenaya Lake, at a comparable altitude on the western slope of the range.

A comparative study of the races in the Stanford garden leads to the conclusion that the forms from east of the Sierran crest are morphologically fairly distinct from those of the west side. Unfortunately, transportation restrictions during the war prevented the testing of the populations from Conway Summit and Leevining at the Mather and Timberline stations.

THE LEEVINING POPULATION

Leevining lies at the foot of the Sierra Nevada in the arid Great Basin plateau region at 2100 m. elevation. Here are stream-fed meadows, where a variety of herbs and grasses find congenial habitats. The Leevining population was collected in such a meadow 2.5 miles south of the town, a few miles southwest of Mono Lake. On the arid slopes and flats near by are stands of xerophilous shrubs, the dominant species being *Artemisia tridentata* and *Chrysothamnus nauseosus.*

The climate in this area is severe, with very cold winters and short, hot summers. The diurnal variation in temperature is large, as is characteristic of continental deserts. Figure 5 shows the temperature and precipitation curves for Bridgeport, 30 miles north of Leevining at the same altitude in rather similar terrain.

In the garden at Stanford, the Leevining population shows morphological characters like those of the Conway Summit population, having long, narrow, bright-green leaves. It differs in its growth, however, in having a shorter period of winter dormancy, a much greater tendency to flower, considerably taller stems, larger leaves, and generally more vigorous rosettes. Some of these differences are evident in table 1. The Leevining population shows the usual amount of individual variation. Although it was not tested at the two mountain stations, observations made at Stanford show clearly that it belongs to a race distinct from the one at Conway Summit 380 m. higher.

A LATITUDINAL TRANSECT

The forms of *Achillea* that occur across the Sierra Nevada harmonize closely with the climatic factors of their environments, which, in turn, are clearly influenced by altitudinal differences. The Achilleas from very different latitudes, also harmonizing closely with their environments, are equally differentiated. Although the information is much less complete on latitudinal than on altitudinal races, the data available add materially to the general perspective of the *Achillea* picture in western North America.

Three forms from the maritime zone of the Pacific coast are shown in figure 8 as they appear in a uniform garden at Stanford. These are from central California, central Oregon, and Kiska Island in the Aleutian chain. Although each is recognizably different from the others, their similarity is striking in view of their diverse origins.

The winter-active Bodega form from California has already been described on page 16. The plant from Otter Crest, Lincoln County, Oregon, and the one from Kiska grow less actively during the winter at Stanford.
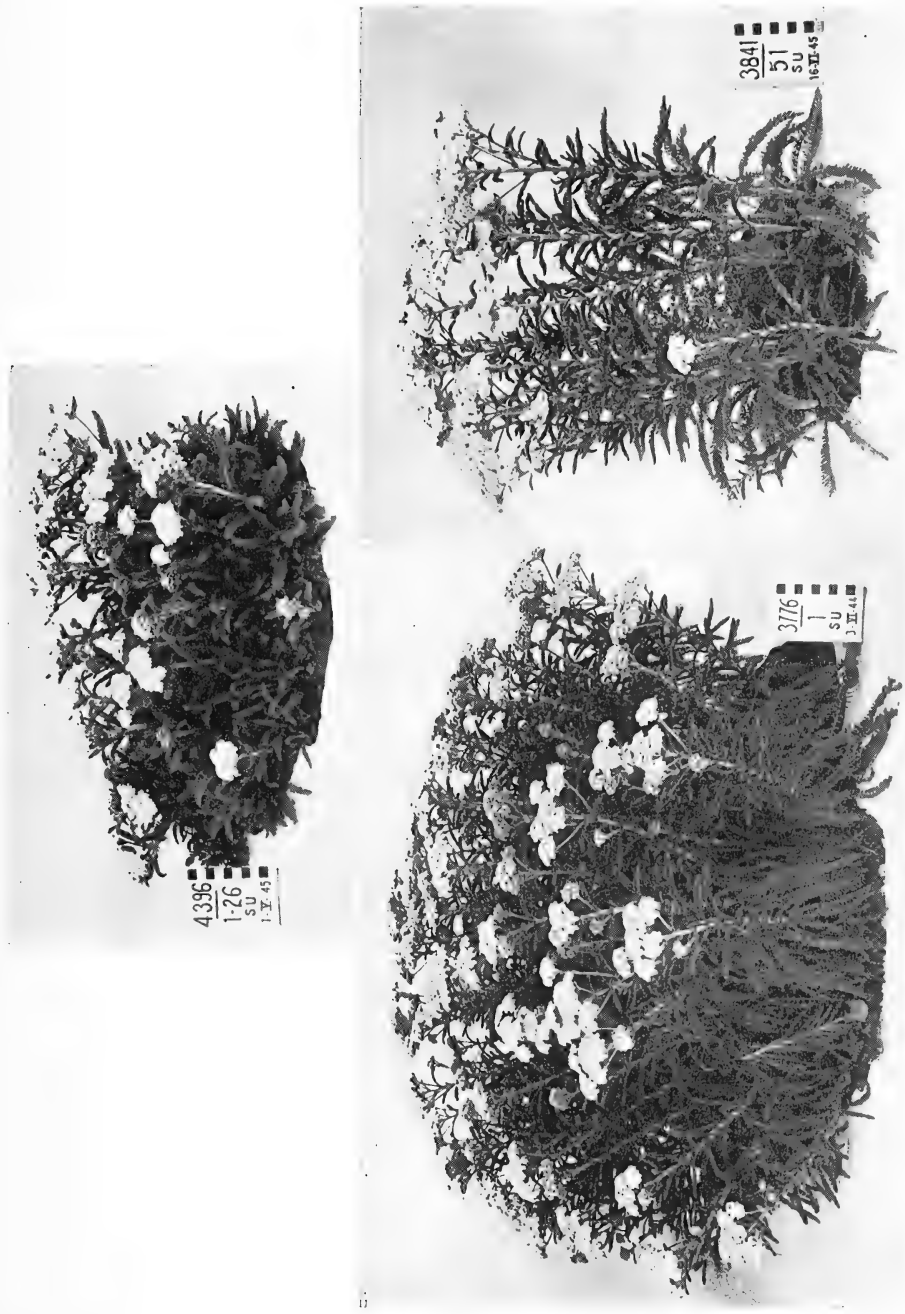
Fig. 8. Maritime forms of *Achillea borealis* from the Bodega coast, central California (left), Otter Crest, central Oregon (right), and Kiska Island (above), grown in the garden at Stanford. The black-and-white scale is 10 cm. high.

The three forms are morphologically connected by series of intermediates, and are hexaploid. From the morphological, cytological, and geographical evidence available, it appears reasonable to include all as members of one species, *A. borealis,* the type locality of which is Sitka. The plant from Kiska develops much more rapidly than the other two, for in the Stanford garden it blooms more than a month earlier (table 1). Differences in winter activity, rate of stem development, and earliness of flowering separate these plants into distinct latitudinal races.

The climate is cooler throughout the year at Otter Crest than at Bodega, and the rainfall is much higher. This may be seen by comparing the climatic data for Point Reyes, shown in figure 2, with those for Newport, a weather station near Otter Crest, in figure 9. At Dutch Harbor, on the eastern end of the Aleutian chain, the still more pronounced drop in temperatures throughout the season (fig. 9) is accompanied by a considerable shortening of the growing season. The climate at Dutch Harbor is probably rather similar to that near sea level at Kiska Island. Point Reyes, Newport, and Dutch Harbor are all maritime stations characterized by small diurnal variations in temperature and relatively equable seasons, but the seasonal differences become more accentuated at the more northern latitudes.

ALTITUDINAL RACES FROM KISKA ISLAND. Kiska is a volcanic cone near the western tip of the treeless, wind-swept Aleutian chain of islands at $52°$ north latitude. The *Achillea* seed material was collected at six localities at and above Kiska Harbor by Mr. Malcolm A. Nobs, while he was serving with the United States Army. At five of the localities, seed from 25 individuals was mixed together in order to obtain a representative sample of the natural variation. In all six localities the plants were still in flower on October 9, 1943, when the samples were taken. The carefully chosen altitudinal series of samples from this isolated, unprotected island is of more than usual interest for the study of population differences, so pertinent data on each colony are detailed below.

4395: Seeds of 25 plants from a sheltered creek bottom at 7 m. elevation. In their native habitat the plants grew to 35 cm. tall with leaves to 25 cm. long.

4396: Seeds of 1 plant from a wind-swept dune at 15 m. This plant was 33 cm. tall with leaves to 20 cm. long.

4397: Seeds of 25 plants from a wind-swept hill at 150 m. The plants were 10 to 20 cm. tall with leaves 5 to 10 cm. long.

4398–4400, inclusive: Seeds of 25 plants each, from colonies at 250, 300, and 365 m. altitude, respectively, on the ridge above Middle Pass overlooking Kiska Harbor. The plants from each colony, growing in a carpet of moist tundra heath, were only 5 to 8 cm. tall with leaves 4 to 6 cm. long.
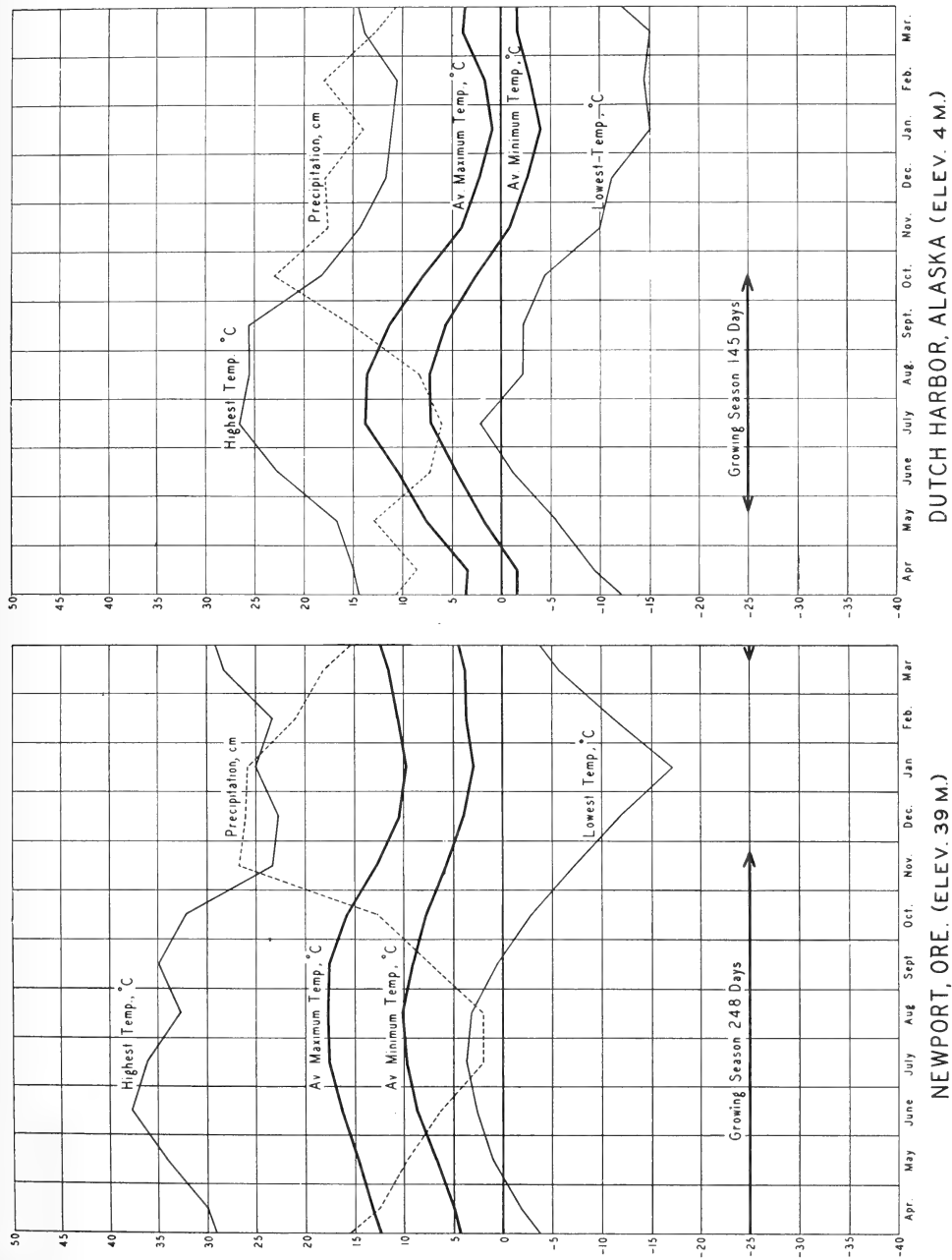
Fig. 9. Temperatures, precipitation, and average growing season (frost-free period) of a maritime station in central Oregon (Newport) and another in Alaska (Dutch Harbor). Based on United States Weather Bureau records for 39 years from Newport, and 7 years from Dutch Harbor.

Mr. Nobs observed that the species occurred to the peak of the island, at about 1200 m., but was unable to revisit this locality to collect material. The extreme alpines are therefore not represented in the material grown at Stanford, although it is difficult to visualize smaller ones than those collected at 250 and 365 m. altitude.

Populations of 30 to 60 plants of each of the six collections were grown at Stanford. With irrigation, they well withstood the great change from
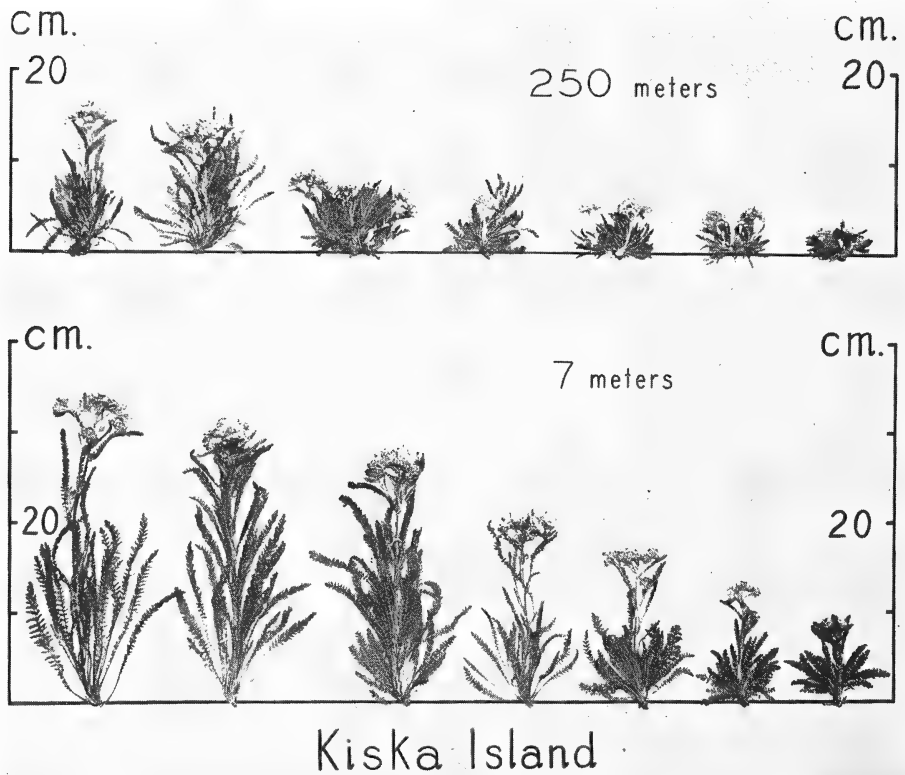
FIG. 10. Comparison of individual variation among plants of two populations from different altitudes on Kiska Island, as shown by specimens taken in May 1945 from a uniform garden at Stanford.

the cold, wet climate at Kiska to the much warmer and drier one at Stanford. They reached almost the same size as on Kiska, showing the same differences between tall plants from near sea level and much shorter ones from higher up. This trend is illustrated in figure 10, which shows samples of 7 plants of two populations, from near sea level and from 250 m. elevation. The much larger size of the former is clearly evident, although the ranges of variation within the two populations overlap. The

diminutive dwarfs found at higher altitudes on Kiska are the smallest Achilleas ever grown at Stanford.

All six Kiska populations can be compared in figure 11 from the graphic representation of the differences in plant height. The frequency graphs are constructed in the same manner as those in figure 1, and the herbarium specimens represent plants of the average height for each population. The two populations from near sea level are much alike and

TABLE 2

Summary of characteristics of Kiska races at Stanford

(Data of 1945—mean values)

Culture number	Altitude	No. of plants	Longest stem (cm.)	No. of stems	Width of inflorescence (cm.)
4395.	7 m.	59	20.0±1.00	12.5±1.09	9.5±0.47
4396.	15 m.	60	23.6±0.60	22.1±1.05	10.8±0.32
4397.	150 m.	60	10.7±0.63	13.8±1.45	7.0±0.42
4398.	250 m.	57	8.8±0.62	9.7±1.23	5.8±0.40
4399.	300 m.	27	7.5±0.66	8.9±1.37	7.5±0.64
4400.	365 m.	31	8.1±0.69	8.3±1.00	5.3±0.41

Culture number	Length of leaves (cm.)	Width of leaves (cm.)	Width of rosette (cm.)	Date of first flowers	Winter dormancy*
4395. . . .	12.20±0.46	1.88±0.06	39.5±1.28	April 18.0±2.24	3.6±0.19
4396. . . .	11.50±0.29	1.99±0.08	39.2±0.79	April 16.7±1.78	2.0±0.12
4397. . . .	8.48±0.32	1.47±0.04	39.4±1.23	April 17.3±2.02	5.5±0.28
4398. . . .	7.92±0.35	1.22±0.05	33.9±1.23	April 21.0±2.33	6.3±0.23
4399. . . .	6.08±0.47	1.13±0.07	26.2±1.79	April 14.3±3.65	7.6±0.29
4400. . . .	6.62±0.49	1.18±0.09	25.4±1.74	April 19.2±2.99	7.6±0.36

*Dormancy rating on a 1–10 scale: 1–5, ±active; 6–10, ±dormant.

definitely taller than the others; the three from 250 to 365 m. altitude are also alike but much dwarfer. The population from 150 m. is intermediate in height. These differences in size are associated with significant differences in the degree of winter activity at Stanford.

As in the Achilleas from the Sierran transect, height is only one character out of many in which the populations vary. Additional information is summarized in table 2, which gives the mean values and standard errors for a number of characters as expressed in the Stanford garden. These means, however, fail to describe the recombinations of characters
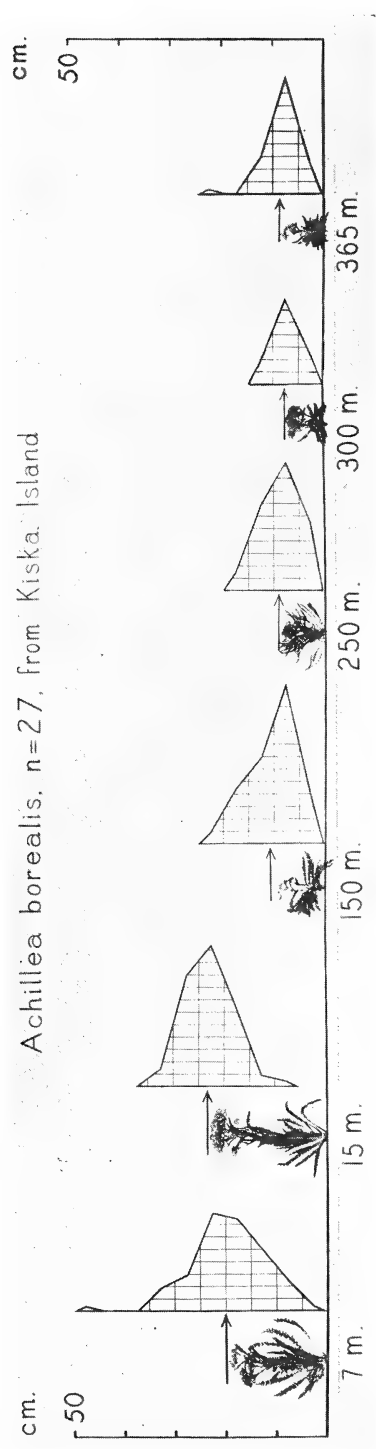
FIG. 11. Frequency graphs showing variation in height among individuals within the populations of *Achillea borealis* from different altitudes on Kiska Island as grown in a uniform garden at Stanford. The spaces between horizontal lines represent intervals of 5 cm.; the spaces between vertical lines, frequencies of 2 individuals. The arrows point to the mean heights, and the specimens represent plants of average height. See also table 2.

observed in individuals of each population. Statistically, the two populations from near sea level are the more floriferous, with wider and taller inflorescences and longer leaves, and they are fairly winter-active. On the other hand, the three populations from the higher altitudes consist of plants with distinctly few short and narrow inflorescences and short leaves, and they are all rated as winter-dormant. They also have grayer, more pubescent herbage than the two populations from near sea level. Some of the high-altitude plants form low, wide mats, with sessile inflorescences starting at the very ground. The population from 150 m. altitude is statistically intermediate as to length and number of stems and winter dormancy, but in its other characteristics conforms with the higher-altitude populations.

The rather clear distinction between the low-level and higher-altitude plants may be related to the relatively abrupt change in climate that takes place at about 150 m. elevation on the island. Above this level snow lies on the ground over a large part of the year, whereas at lower levels the climate is greatly tempered by the sea. The characteristic fog banks seen in views of the Aleutians at approximately the 150-m. level are doubtless associated with the zonation of warm and colder strata of air.

None of the races from Kiska are as winter-active at Stanford as those from the coast of California. Those from near sea level at Kiska never become completely dormant, but those from 150 m. and above are dormant for as long as two months, the individuals varying as to the length of the period. When the rest period is over, the forms from higher altitudes develop short flowering stems so rapidly that they overtake those from near sea level, and the dates of flowering actually observed at Stanford are about the same for all.

All populations are variable as are those from California. The variation includes, besides height, the number and size of inflorescences, size of ligules, number of disk florets, flower color (white to pink), size and pubescence of leaves, extent of rhizomes, general vigor, and length of winter dormancy. Some of these variations show correlation with altitude, others do not. Some recombination of these characters was observed in all the populations, indicating that gene exchange takes place both within and between populations. From the seed collected at the highest altitude one fairly typical low-altitude plant was obtained, and a few of the seeds from near sea level developed into plants of the high-altitude type, suggesting that wind transport may play a role in the mixing of populations.

Even with such extensive variation, at least two statistically distinct climatic races or ecotypes can be recognized among the Achilleas

from Kiska. Their presence in this telescoped series of populations suggests that strong selection is constantly operating in these rigorous environments.

RACES FROM NORTHERN EUROPE

Achillea millefolium L. is widely distributed in Eurasia, extending from the Mediterranean region and northern Persia to the Arctic Circle and even farther north. Forms from Denmark and Swedish Lapland have been included in the present experiments for comparison with western North American representatives of this species complex. *Achillea mille-folium* is hexaploid, as is the North American *A. borealis,* with $2n=54$ chromosomes, as was shown by the writers (1940). The forms of *mille-folium* from Denmark and Lapland differ in appearance from the North American Achilleas, being less pubescent, and having smaller, generally darker-green leaves with fewer and wider segments.

The Danish maritime Achilleas used in these experiments were seedlings from a single plant from a sandy, exposed seashore on the west side of Sjaelland near Skelskör at latitude 55° 17′ N. In this grass-covered habitat the Achilleas were depressed, 10 to 20 cm. in height, and of an early-flowering type. The population of 29 individuals at Stanford varied between 14 and 57 cm. in height, and proved to be winter-active and early-flowering. These plants, like those from the coast of California, continued to grow during the entire summer period. Differences between this Danish ecotype from the seacoast and a taller, later-flowering woodland form have already been described by the writers (1940).

The Danish races were collected within the zone of the cold temperate western European deciduous forests, and the Lapland race was obtained at the point where the subarctic birch replaces the coniferous forests of central and northern Scandinavia. The material of the Lapland race was taken from a small colony growing along a railroad embankment near Abisko, Sweden, at latitude 68° 20′ N. in an area rich in vegetation. The Achilleas, presumably not native in northern Sweden, were found only in this locality of disturbed ground and were well established and 40 cm. high. Nevertheless, seedlings grown at Stanford had the characteristics of a subarctic ecotype, reacting differently from the Danish forms from 13° farther south. In this garden, where the Lapland form is winter-dormant and considerably reduced in size, the Danish form is continuously active and increased. Growth of the Lapland form resumes in March, and the stems develop quickly so that some plants are in flower a month later. As is true of most of the races from high latitudes and altitudes, its flowering at Stanford is erratic and extends over a long period.

As will be seen in chapter III, the reactions of the Danish and Lapland races at the mountain stations are similar although they have a pattern distinct from that of any of the California races.

SURVEY OF THE CLIMATIC RACES

The transect across central California from the coast to the Great Basin traverses a great variety of environments and climates, and the members of the *Achillea millefolium* complex follow this transect without interruption. Perhaps no other species complex of higher plants has so complete a representation of forms here. When samples from intervals along this and other transects are brought together and compared in one environment, as in the uniform garden at Stanford, their differences stand out. The species complex is composed of many genetically and ecologically distinct races, and these, in turn, are composed of many variable populations. For a survey of all the populations studied, the reader is referred to table 1, pages 9–10.

A late-flowering, evergreen, maritime form of characteristic low, dense habit grows in that narrow zone subjected to the force of salt winds sweeping the bluffs immediately above the sea. In less exposed places, but still on the seaward side of the outer Coast Range, is an equally evergreen and late-flowering but taller race. Many transitions between the two occur. On well drained sand dunes, where the ground warms up quickly after the winter rains, populations like those from San Francisco, Año Nuevo Point, and Seaside tend to flower earlier than the others.

A third race occupies the inner Coast Ranges, their intervening valleys, and the foothills that surround the Great Valley. This foothill race is fitted for growth during the mild, rainy winters and escapes the long dry period by blooming quickly (starting in March or early April) and then becoming dormant through the summer and fall months. Differences between populations exist also in this race, and are possibly augmented by gene exchange with the coastal races.

In the San Joaquin Valley bottom lands there is a giant race capable of making effective use of the intense solar radiation, high summer temperatures, ample moisture, and long growing season there. This race is essentially evergreen at Stanford.

The climate in the Sierras changes rapidly with increasing altitude. Near the lower borders of the timber belt it makes a transition from conditions that permit winter growth to those in which freezing temperatures enforce winter dormancy. The tetraploid forms of *Achillea* from 915 m. altitude in this transitional region and those from warmer slopes at some-

what higher altitudes are winter-active when grown in the mild coastal climate at Stanford, behaving much like forms from the Coast Ranges. With increasing altitude, the climate becomes colder and the growing season shorter. Populations from the higher elevations become winter-dormant even at Stanford. Their size decreases as the altitude increases. Up to about the 2000-m. mark they become successively later-flowering at Stanford, but above 2000 m. the trend is reversed, for from this point to the summit they flower successively earlier, with the high alpine from 3350 m. the earliest of any Sierran race. Any one sample contains individual variation sufficient to overlap samples from neighboring elevations. The mode for any character with selective value shifts from population to population paralleling climatic shifts, but the variation within populations is so great that the impression is given of a continuous gradient. The tiny alpine form from 3350 m. culminates a trend that has produced strikingly different extremes.

On the eastern slope of the Sierras, in the Mono Lake basin, at 2480 and 2100 m., two races are found that are late-flowering and adapted for the severe, arid, continental climate there.

In northern California the familiar maritime form of *Achillea borealis* occurs on the immediate coast. Taller forms, very similar in aspect and behavior to the taller coastal forms from central California, extend inland across several watersheds to central Trinity County. Counterparts of the foothill and Great Valley races are not found. Instead, the tetraploid *A. lanulosa* extends westward, invading the domain of the hexaploid, with one tall, winter-active representative, having the same periodicity as neighboring hexaploids, in the heart of the redwood region near Dyerville (table 1, p. 10). This form is quite different from the winter-active tetraploids in the lower Sierra Nevada. The tetraploids from the Cascade-Sierran axis in northern California become increasingly winter-dormant at Stanford.

The maritime hexaploid race, following the coastal strip, has been traced through Oregon. Plants of maritime appearance have also been traced, by herbarium specimens, along the coast through British Columbia to Alaska and the Aleutians. The taller hexaploids were found in the coastal plain at North Bend, Oregon, and Chehalis, Washington, but somewhat removed from the immediate coast. In the Oregon Coast Ranges it appears that this form is largely replaced by tall tetraploids that are similar to the form from Dyerville and as winter-active as the coastal hexaploids.

The tetraploid extends out to the very coast at Port Orford, Oregon,

and there on exposed headlands occurs as a maritime ecotype that is morphologically so parallel to the hexaploid that its tetraploid nature was not suspected before the chromosomes were counted. This form is illustrated in figure 12. Its striking similarity to the maritime hexaploid is evident from a comparison of this figure with figure 8.

Farther inland toward the Cascades in Oregon, and at higher altitudes, tetraploid forms were obtained at Gold Hill and Prospect that behaved like the winter-active Groveland and Mather populations, and on the

Fig. 12. A maritime form of the tetraploid *Achillea lanulosa,* with $n=18$ chromosomes, from Port Orford, Oregon, grown in the garden at Stanford. Note the similarity to the maritime hexaploid forms shown in figure 8.

summit of Mount Ashland another corresponding to the winter-dormant, late-flowering Aspen Valley form. At Squaw Butte, east of the Cascades, was found the Great Basin counterpart of the Leevining population from east of the Sierra Nevada. The full range of diversity of the Achilleas from the Pacific Northwest, however, is still unknown.

At Kiska, the coastal forms are morphologically closely related to the maritime hexaploids of Oregon and California, as can be seen in figure 8, but they flower much earlier and so belong to a different ecotype (table 1). The forms from higher altitudes on that island are distinct from any other race, constituting a high-latitude, alpine ecotype. The coastal race

4

from Seward, Alaska, in a more northern, more continental climate, is distinctly winter-dormant at Stanford, and differs in that respect from the Kiska coastal race.

Races of *Achillea millefolium* from northern Europe show similar differences. Two Danish races are continuously active and late-flowering at Stanford, whereas a subarctic race from Lapland is distinctly winter-dormant yet early-flowering. Turesson (1930) reported differences in earliness of one week in forms from central Europe and southern Sweden, and appreciable differences in height between a Swedish form and a giant race from the fertile Siberian steppe near Omsk, at nearly the same latitude. These samples, however, are too few and scattered to provide a picture of the ecotypic composition of *A. millefolium* in Eurasia.

III

RESPONSES OF RACES IN THREE CLIMATES

When climatic races from many diverse environments are brought into one garden, we see their genetic differences expressed under one set of conditions. This is an important first step in comparing them, because the complicating factor of modification is eliminated. The hereditary differences between populations may be observed in conjunction with the hereditary variation within them.

From the very nature of our problem, however, it is not sufficient to study forms from different climates in only one environment. If we are to understand more fully why these races occur where they do, we need to know how they perform under as wide a range of conditions as that occupied by the species complex to which they belong. Otherwise, our knowledge of their capacities would remain incomplete, for in any one environment only certain races attain fullest expression. This is more clearly seen when identical populations from a series of climatic races of a species are compared in contrasting environments like the Stanford, Mather, and Timberline transplant stations.

The value of this method of study is very well illustrated by the various races of *Achillea* from the west-east transect across central California. At Stanford, the coastal, foothill, and San Joaquin Valley populations are best developed; at Mather, the races from between Groveland and Yosemite Creek grow best; and at Timberline, only forms from Tenaya Lake and above are able to mature. The differences between all the races cannot be fully realized at any one station.

By comparing the various climatic races in different sets of environments, we provide, in effect, a third dimension to the general picture of their differences. The first conclusion gained from comparing them in only one environment is valuable in estimating the range of variability in each race, but the potential capacities of the individual races are not thereby disclosed. The three transplant stations serve as a climatic sieve by which the populations may be sorted into distinguishable ecological units.

Approximately 30 individuals of each of fourteen populations were divided into three parts and planted in the gardens at Stanford, Mather, and Timberline in 1942. As was mentioned in chapter I, these plants were selected from a random sample of 60 seedlings which had been grown at Stanford from seed collected in the wild. The technique employed was

the same as that earlier applied to numerous herbaceous species used in the varied-environment experiments, described in detail by the writers (1940).

Organized data on the individuals of each population were collected from the three environments over a three-year period. Many observations were made throughout each year at Stanford, representing one climatic extreme, but ordinarily only two or three sets of observations were possible during the short growing season at Timberline, representing the other. Length and number of stems, date of first flowers, width of rosettes, general vigor, and seasonal development at various times of the year were recorded in detail for each division. The effects of frosts, particularly at the mountain stations, were also recorded. This record was supplemented by full-sized herbarium specimens and photographs of living plants. The present report is based on a study of these factual materials.

THE TRANSPLANT STATIONS. A description of the Stanford, Mather, and Timberline stations, with photographs of the gardens, has already been published (1940). Some of the salient contrasting features of these stations which give an impression of their very different climates are summarized in table 3.

The weather data for Timberline in this table are based on United States Weather Bureau records from Ellery Lake, 3 miles away and 150 m. lower in elevation. The weather at Ellery Lake is milder than at Timberline, for, as is shown in table 4, readings on a minimum thermometer located at ground level in the Timberline garden were found to average 4.6° lower during the growing season than those at Ellery Lake.

Minimum temperatures differ within short distances in Slate Creek Valley, where the gardens are located. A second minimum thermometer placed on a slope some 20 m. higher than the garden and a short distance away recorded consistently higher temperatures than the garden thermometer. The average increases on the slope, as computed from data comparable with those used in table 4, were as follows: $3.77 \pm 0.21°$ C. for July, $3.72 \pm 0.21°$ C. for August, and $3.28 \pm 0.20°$ C. for September. On quiet nights the colder air drains into the valleys, leaving the hillsides relatively warmer. Such differences produce micro-environments and accordingly affect plant distribution. The south-facing warmer slopes are occupied by a forest of *Pinus Murrayana* and many herbaceous plants characteristic of lower altitudes, whereas the floor of the valley below the slope is occupied by true subalpines.

TABLE 3

Comparison of the transplant stations

	Stanford*	Mather†	Timberline‡
Location......................	between the outer and inner Coast Ranges	western slope of the Sierra Nevada	east of the Sierran crest
Elevation (m.)....................	30	1400	3050
Natural vegetation...............	oak-grass savanna	coniferous forest	alpine
Average growing season (days)......	283	145	67
Winter snowfall..................	none	moderate	very heavy
Native Achilleas' most active period	December to July	May to July	August
Highest recorded temperature (°C.)..	40.6	39.4	28.3
Lowest recorded temperature (°C.)..	−5.6	−21.7	−31.7
Average January temperature (°C.)..	8.14	2.25	−10.10
Average July temperature (°C.).....	18.64	21.42	12.84
Average annual precipitation (cm.)..	38.99	103.02	78.31

*Weather data from Palo Alto.
†Weather data from Lake Eleanor
‡Weather data from Ellery Lake.

TABLE 4

Comparison of summer minimum temperatures at Ellery Lake (elevation 2890 m.) and Timberline garden (elevation 3050 m.)

Month	No. days' observations*	Av. min. temp. at Ellery Lake (°C.)	Av. min. temp. at Timberline (°C.)	Difference, Ellery Lake minus Timberline (°C.)
July.............	39	6.55	1.89	4.61±0.385
August..........	58	5.84	1.22	4.67±0.281
September.......	57	2.11	−2.55	4.66±0.354

*Observations at the two stations during a four-year period, 1939–1942 inclusive, made on the same days.

THE BODEGA AND SAN GREGORIO POPULATIONS

These two forms from the coast of central California respond similarly to the environments of the mountain stations and can therefore conveniently be discussed together. It will be recalled that both were evergreen in the garden at Stanford, as in their native habitats. Consequently, the conditions at the mountain stations test their capacity for adjustment severely.

At Mather, both populations are forced into a long winter dormancy that is broken in early spring, but the new growth is relatively weak, as

though dormancy had caused the plants to deplete their food reserves. This weakness is overcome as the season advances. Although these coastal populations are more frost-resistant than the native Mather Achilleas, late spring freezes, such as occurred in 1943, may injure the young leaves and stems, temporarily weakening the plants.

Although the coastal plants flower at Mather during July, the majority continue in active growth through August, after the foothill forms have become summer-dormant, and September, well after frosts have appeared. Their ability to withstand moderate freezing temperatures, which is of importance to them in their native habitats, where they grow most actively during the winter season, is generally greater than that of the Sierran plants. In October, however, the temperatures at Mather drop too low to permit further growth of even the coastal populations, and the leaves turn bronze and then black as the weather grows colder.

Two important characteristics of the coastal plants that become evident in the Mather garden are their slow rate of growth through spring and early summer, with consequently belated flowering, and their active development of new growth in August and September. Their acceleration is slower than that of the Sierran races, reflecting their different genetically controlled physiological make-up. Yet despite this tendency, they are able to adapt themselves to the change in seasons well enough to survive with some degree of success.

The total growth made by the coastal forms at Mather is considerably less than that at Stanford. One reflection of this is the difference in height at the two stations, as shown in figure 13. In this figure the relative performances of 7 typical plants of the San Gregorio population at Stanford, Mather, and Timberline are shown. In the bottom row are herbarium specimens of a sample that covers rather well the range of variation in height found in this population at Stanford. In the middle row, arranged in the same sequence, are specimens from divisions of the same plants grown at Mather. It is obvious that each plant at Mather has decreased in size, when Mather and Stanford are compared, but not all have decreased in the same proportion. The top row shows that almost all died at Timberline.

Additional information concerning the responses of the coastal populations to the mountain environments is given in tables 5 and 6, in which length and number of stems, and date of first flowers are recorded for each propagule at each station. The plants in figure 13 can be traced in table 6 by their plant numbers. It is apparent that the heights of these plants at Mather have very little relation to their relative heights at Stanford. The
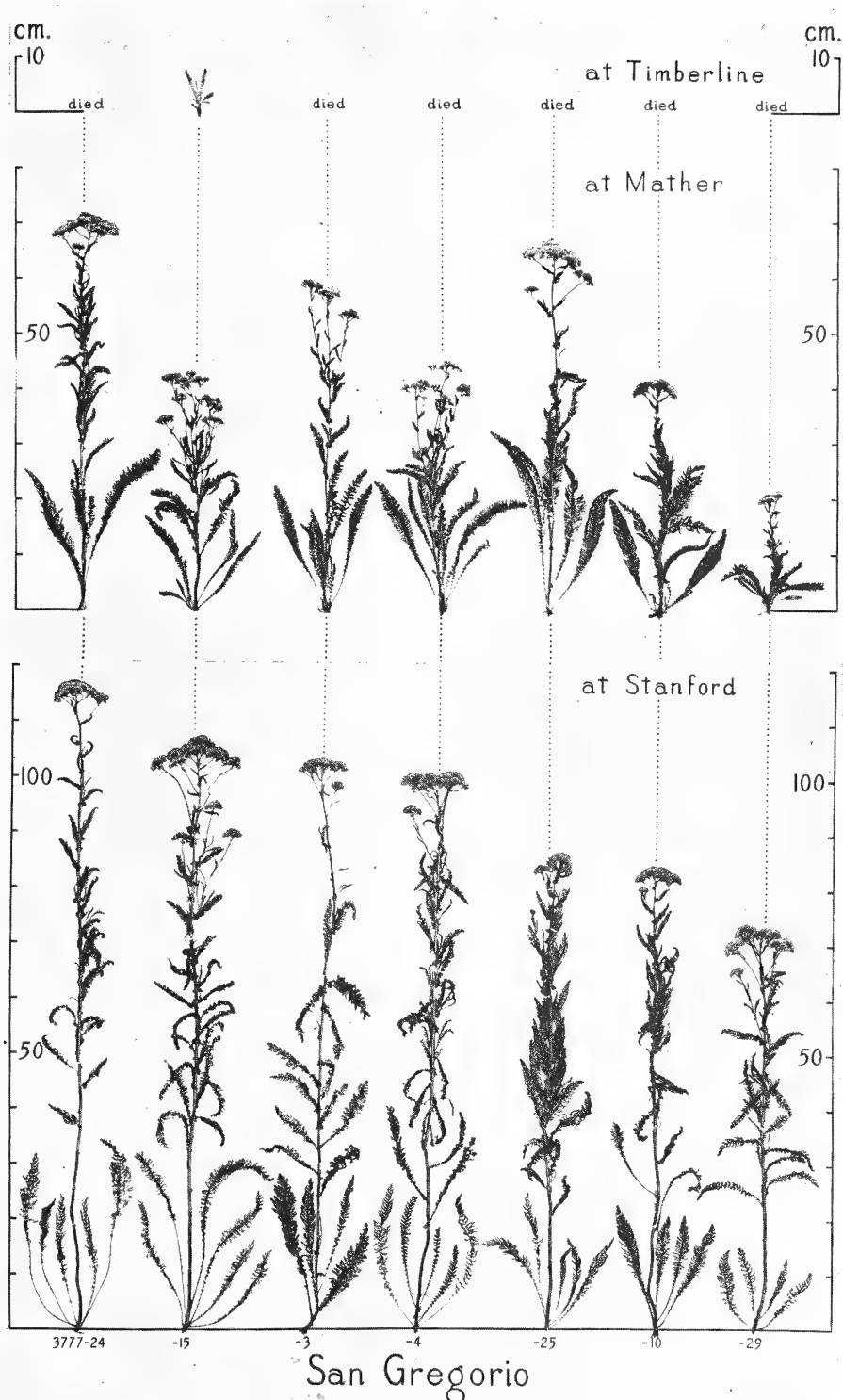
FIG. 13. Responses of clones of 7 plants of the coastal San Gregorio population (elevation 50 m.) at Stanford, Mather, and Timberline. The dotted lines connect herbarium specimens from members of the same clone at the three stations. The numbers at the bottom are those of the individual plants; their records may be traced further in table 6.

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TABLE 5

REACTIONS IN THE BODEGA POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS	
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather
3776- 1...	52	25	D-1	27.0	2.3	....	May 19.5	July 5
- 2...	48	33	D-3	34.5	39.3	0.0	May 21.5	July 6.5
- 3†..	67	53	D-1	34.0	39.0	....	May 28.5	July 12
- 4†..	61	40	D-2	15.5	22.3	0	May 14.5	June 28.5
- 5...	57	29 (D-3)	D-1	20.0	17.0	....	May 6	July 10
- 6...	48	38	D-2	21.0	12.3	0	May 18	July 12.5
- 7...	38	23	D-1	22.0	13.3	....	May 22	July 20
- 8...	37	20	D-1	3.5	9.0	....	May 24.5	July 13
- 9...	54	33	D-2	29.0	16.0	0	May 23.5	July 18
-10...	48	23 (D-3)	D-1	18.0	18.5	....	May 7	July 9
-11...	43	23	D-1	15.0	7.7	....	May 26.5	July 23
-12...	48	34	D-1	31.5	10.3	....	May 22	July 21.5
-13...	48	38 (D-3)	D-1	19.5	15.0	....	May 19	July 11
-14...	49	39	D-1	23.5	21.7	....	May 31.5	July 9
-15...	47	17 (D-1)	D-1	10.0	2	....	May 7.5	July 6
-16...	54	35	D-2	28.5	10.7	0	May 21	July 23.5
-17...	46	25 (D-2)	D-1	17.5	20	....	May 29.5	July 6
-18†..	37	21	D-1	18.5	8.3	....	May 21	July 13
-19...	52	50	D-1	14.0	64.0	....	May 19	July 3
-21...	65	34	D-2	15.0	24.3	0	May 4.5	June 25
-22...	69	41	D-1	31.5	23.0	....	May 22	July 7.5
-23...	40	35	D-1	7.0	47.0	....	June 8	July 9
-24...	45	29	D-1	8.5	9.3	....	June 15	July 10
-25†..	42	21 (D-1)	D-1	7.0	3	....	May 29	July 12
-26...	63	D-1	D-1	5.5	....	....	June 13.5	....
-27†..	42	35	D-1	15.5	32.7	....	May 26	July 10.5
-28†..	30	18	D-1	14.0	0.3	....	May 15	Aug. 4
-29†..	22	34	D-1	22.5	21.3	....	May 14	June 28.5
-30...	50	18 (D-3)	D-1	15.5	18.0	....	Apr. 18	June 27
-31...	65	D-3	D-1	33.5	0	....	May 22.5	....
Total.....	30	28	....	30	29	6	30	28
Means....	48.9	30.8	....	19.27	18.19	0.00	May 21.1	July 11.5
	±1.98	±1.78		±1.64	±2.74		±2.15	±1.67

†Plants illustrated in figure 6.

Explanation of tables 5 to 18:

Longest stems: maximum length observed for years 1941–1944 at Stanford, and 1943–1945 at Mather and Timberline.

Number of stems and Date of first flowers: mean values for two years at Stanford and three years at Mather and Timberline.

D-1: died first winter, no data; D-2, D-3, D-4: died the second, third, and fourth winters, respectively.

TABLE 6

REACTIONS IN THE SAN GREGORIO POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS	
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather
3777- 1†..	111	70	D-1	15.0	2.7	....	Apr. 25.0	July 5.0
- 2...	110	80	D-1	39.0	40.0	....	May 2.5	July 4
- 3*..	113	58	D-1	25.5	14.3	....	May 5.5	July 8.5
- 4*..	101	57	D-1	28.5	22.3	....	Apr. 29.5	July 8
- 5†..	115	69	D-1	76.5	30.3	....	Apr. 30.5	July 7
- 6...	98	71	D-2	39.5	30.0	0	May 15	July 15
- 7†..	96	51	D-1	25.5	25.7	....	Apr. 23.5	July 2
- 8...	91	48	D-1	18.0	22.3	....	May 17	July 27
- 9...	116	52	D-1	17.5	14.3	....	May 7.5	July 8.5
-10*..	83	74	D-1	26.5	43.3	....	May 15	July 4.2
-11...	79	53	D-1	35.5	10.0	....	May 7	July 6.5
-12...	99	58	D-1	34.5	8.7	....	May 3.5	July 7.5
-13...	122	45	D-1	26.5	11.0	....	May 1	July 26.5
-14...	120	84	D-1	65.0	22.3	....	May 3.5	July 28
-15*..	115	59	D-3	35.5	12.0	0.0	Apr. 30	July 7
-16...	109	D-2	D-4	23.5	0	0.0	Apr. 25	....
-17...	96	D-1	D-2	58.5	....	0	May 18	....
-18...	84	D-2	D-1	38.0	0	....	Apr. 30	....
-19...	96	37 (D-2)	D-2	24.0	34	0	Apr. 29	July 2
-20...	70	44	D-1	13.5	6.7	....	Apr. 28.5	July 16.5
-21...	116	73	none	48.5	15.3	0	May 10	July 8
-22...	108	71	D-1	36.0	24.3	....	Apr. 23.5	July 1.5
-23...	109	56	D-1	24.0	20.3	....	May 5	July 5
-24*..	119	71	D-1	24.5	41.3	....	May 13.5	July 11.5
-25*..	88	63	D-2	18.0	25.7	0	May 25	July 12
-26†..	97	73	D-1	15.5	12.3	....	May 27.5	July 12.5
-27†..	65	61	D-1	21.0	27.3	....	May 21.5	July 1.5
-28†..	78	38	D-2	23.5	11.0	0	May 9.5	July 12
-29*..	.75	46	D-1	21.0	14.7	....	May 19	July 11
-30†..	63	45	D-1	29.0	34.7	....	May 1.5	July 5
Total.....	30	27	....	30	29	8	30	27
Means....	98.0	59.5	....	30.90	19.89	0.00	May 7.8	July 10.7
	±3.14	±2.49		±2.73	±2.26		±1.73	±1.42

†Plants illustrated in figure 6.
*Plants illustrated in figure 13

TABLE 7

REACTIONS IN THE CLAYTON POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS	
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather
3965- 1...	68	D-1	D-1	9.3	....	....	Apr. 8	....
- 2...	79	D-2	D-2	21.3	0	0	Apr. 18.5	....
- 3...	68	33	D-1	18.0	6.7	....	Apr. 4.5	June 12
- 4...	74	28 (D-3)	D-1	12.0	7.5	....	Apr. 3.5	June 15
- 5...	69	43 (D-3)	D-1	19.7	19.0	....	Apr. 10.5	June 11
- 6...	55	D-1	D-2	12.3	....	0	Apr. 11.5	....
- 7...	61	47 (D-3)	D-1	15.7	11.5	....	Apr. 5.5	June 14
- 8...	65	36	D-2	17.7	1.7	0	Mar. 30.5	June 13
- 9...	59	D-2	D-1	9.3	0	....	Apr. 3.5	....
-10...	72	D-2	D-3	15.3	0	0.0	Apr. 10	....
-11...	76	30 (D-2)	D-1	17.0	2	....	Apr. 24	June 20
-12...	77 (D-3)	44	D-1	12.0	4.0	....	Mar. 28	June 5
-13...	84	50	D-2	19.3	4.7	0	Apr. 1	June 16
-14...	71	42 (D-2)	D-1	20.0	16	....	Apr. 13	June 10
-15...	78	37 (D-3)	D-1	21.0	12.0	....	Apr. 14.5	June 10
-16...	64	22 (D-2)	D-2	12.0	3	0	Apr. 7	June 10
-17...	72	33	D-3	10.0	4.0	0.0	Apr. 10	July 13
-18...	79	48	D-3	18.3	20.0	0.0	Apr. 9	June 12.5
-19...	63	42	D-1	15.0	9.0	....	Apr. 5.5	June 30.5
-20...	73	35	D-2	26.3	3.7	0	Apr. 19.5	June 9
-21...	82	43 (D-3)	D-1	21.0	4.5	....	Apr. 10	July 8*
-22...	76	41	D-2	38.7	15.7	0	Apr. 20.5	June 16.5
-23...	59	32	D-1	11.7	6.0	....	Apr. 25	June 10
-24...	69	57	D-1	8.0	9.3	....	Apr. 23.5	June 11
-25...	75	31	D-1	12.3	5.3	....	Apr. 17	June 20.5
-26...	83	46	D-1	8.3	8.7	....	Apr. 18	June 25.5
-27...	75	45	D-1	22.7	14.0	....	Apr. 14	June 20.5
-28...	65	33	D-1	23.0	8.0	....	Apr. 14	June 18
-29...	49 (D-3)	13 (D-2)	D-1	7.5	6	....	Apr. 15	June 10
-30...	62	22 (D-2)	D-2	7.7	8	0	Apr. 22.2	....
Total.....	30	25	....	30	28	11	30	23
Means....	70.0	37.3	....	16.08	7.51	0.00	Apr. 12.8	June 16.8
	±1.57	±1.99		±1.24	±1.05		±1.38	±1.73

*Plant abnormally delayed by frost injury, not included in mean.

TABLE 8

REACTIONS IN THE KNIGHTS FERRY POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS	
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather
3966- 1...	78	D-1	D-1	14.7	....	....	Mar. 29.5	....
- 2...	77	28 (D-2)	D-1	34.7	17	....	Apr. 12.5	June 15
- 3*..	68	48 (D-3)	D-2	14.7	10.0	0	Apr. 17.5	June 15
- 4...	77	D-3	D-1	12.7	0.0	....	Apr. 23.5	....
- 5*..	74	46 (D-3)	D-1	13.0	7.0	....	Apr. 30.5	June 15
- 6...	69	36 (D-2)	D-2	37.0	22	0	Apr. 8	June 10
- 7...	85	37 (D-2)	D-2	27.0	8	0	Apr. 16.5	June 10
- 8...	73	28 (D-2)	D-1	29.7	14	....	Apr. 11	June 10
- 9...	99	18 (D-2)	D-2	24.7	4	0	Apr. 16	June 10
-10*..	99	35 (D-2)	D-2	29.3	2.0	0	Apr. 6	June 19
-11...	69	33 (D-2)	D-1	25.0	23	....	Apr. 9.5	June 10
-12*..	88	18 (D-2)	D-1	17.7	8	....	Apr. 10	June 10
-13...	92	27 (D-3)	D-2	30.7	4.5	0	Apr. 8	June 5
-14...	77	D-1	D-1	47.3	....	....	Apr. 17.5	....
-15...	76	40 (D-3)	D-2	22.3	7.5	0	Apr. 24.5	June 11
-16*..	48 (D-3)	39 (D-3)	D-2	15.5	8.5	0	Apr. 15	June 10
-17...	90	25	D-3	18.0	2.0	0	Apr. 17	June 25
-18...	67	49 (D-3)	D-2	19.5	2.5	0	Apr. 15	June 11
-19...	87	29 (D-2)	D-1	22.0	2	....	Apr. 1.5	June 25
-20*..	119	44 (D-3)	D-3	48.3	4.3	0.0	Apr. 24.5	June 18
-21...	81	36 (D-3)	D-1	35.7	4.5	....	Mar. 26.5	June 13
-22...	88	31 (D-3)	D-1	27.3	6.0	....	Apr. 10.5	July 6
-23...	71	48 (D-3)	D-1	22.0	13.5	...:	Apr. 22	June 13
-24...	88	41	D-1	24.0	8.0	....	Apr. 7.5	June 15.5
-25...	75	44 (D-3)	D-1	18.0	11.0	....	Apr. 5	June 9
-26*..	69	38 (D-3)	D-2	23.3	10.5	0	Apr. 23.5	June 17
-27...	84	48	D-1	29.3	19.3	....	Apr. 22	June 18.5
-28...	79	32	D-1	21.0	2.3	....	Apr. 15	June 18
-29...	70	46	D-2	24.0	11.0	0	Apr. 19.5	June 13
-30...	65	44	D-1	21.0	9.3	....	May 8.5	June 15
Total.....	30	27	....	30	28	13	30	27
Means....	79.4	36.6	....	24.98	8.63	0.00	Apr. 15.7	June 14.7
	±2.40	±1.74		±1.62	±1.15		±1.71	±1.23

*Plants illustrated in figure 14.

TABLE 9

REACTIONS IN THE GROVELAND POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
3967- 1......	86	41 (D-3)	D-2	20.7	4.5	0	May 15	July 2.0	....
- 2......	93	62	D-2	14.0	20.3	0	May 13.5	July 4.5	....
- 3......	77	61 (D-3)	D-2	8.7	39.5	0	May 11	June 27	....
- 4*....	111	72	23 (D-3)	19.3	24.3	2.0	May 8	June 23.5	Sep. 5
- 5......	94	60 (D-3)	15 (D-3)	14.3	17.5	1.7	May 16	June 25	Sep. 20
- 6*....	83	55	D-2	16.3	14.3	0	Apr. 15	June 29	....
- 7......	87	55	9 (D-3)	20.7	8.7	1.5	May 12	June 27.5	Sep. 21
- 8......	69	36 (D-3)	D-2	15.7	15.0	0	May 29	June 29	....
- 9......	75	53	9 (D-3)	5.0	14.0	1.0	June 2.5	June 30	Sep. 20
-10......	69	62	7 (D-3)	8.3	7.0	0.5	May 29.5	July 3	Sep. 20
-11*....	98	72	5 (D-2)	21.3	13.0	0.0	May 6	June 17.5	....
-12*....	87	29 (D-3)	24 (D-4)	12.5	3.5	3.3	May 7.5	July 8	Sep. 13.7
-13......	79	60	D-3	12.3	21.3	0.0	May 19.5	June 26	....
-14......	77	45	24 (D-4)	17.0	14.0	1.5	May 8.5	June 28	Sep. 16
-15......	76	62	30	17.3	15.0	2.0	May 15	June 28.5	I
-16......	93	72	D-2	13.3	21.3	0	May 20.5	June 19.5	....
-17......	81 (D-3)	D-1	D-1	14.0	....	...	May 15	....	....
-18......	69	49	D-2	10.7	13.3	0	May 24	June 28.5	....
-19*....	61	73	D-3	9.7	7.0	0.0	May 15	July 1	....
-20......	86 (D-3)	69	17 (D-4)	17.5	41.3	0.3	May 15	June 19	Sep. 9
-21......	88	58	9 (D-2)	11.7	39.3	1	May 19.5	June 25	Sep. 20
-22......	108	65	D-1	13.3	23.0	...	May 13.5	June 19	....
-23......	99	64	D-1	10.0	17.0	...	May 13	June 15.5	....
-24*....	73 (D-3)	58	D-2	7.5	33.7	0	May 24	June 29	....
-25*....	86 (D-3)	65	D-3	29.0	58.7	0.0	May 1	June 24.5	....
-26......	70 (D-3)	60	D-4	12.5	39.3	0.0	May 15	June 24.5	....
-27......	84 (D-3)	63	D-2	14.0	61.0	0	Apr. 25	June 23.5	....
-28......	84	51 (D-2)	14 (D-4)	37.3	25	2.7	May 25.5	June 25	Sep. 20
-29......	76 (D-3)	56	D-4	30.5	27.0	0.0	May 5	June 22	....
-30......	90 (D-3)	D	none	18.0	....	0.0	May 5	....	....
Total........	30	28	12	30	28	27	30	28	10
Means.......	83.6	58.2	15.5	15.75	22.81	0.65	May 13.8	June 26.2	Sep. 16.5
	±2.12	±2.03	±2.36	±1.27	±2.84	±0.19	±1.88	±1.00	±1.76

*Plants illustrated in figure 15.
I=Flowering stems very immature.

TABLE 10

REACTIONS IN THE MATHER POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
3778- 1	89	70	D-1	18.0	18.0	...	May 21.5	July 2.0	....
- 2	80	83	20	9.0	25.3	0.7	May 10.0	June 29.0	Sep. 28.5
- 3	87	100	D-2	1.0	34.0	0	May 14.5	June 19.5	....
- 4	61	85	D-1	7.5	40.3	...	May 2	June 21.5	....
- 6	101	92	D-1	12.0	34.0	...	May 11.5	June 27	....
- 7	93	82	D-3	10.5	46.3	0.0	May 3	June 28	....
- 8	78	88	D-1	24.5	36.3	...	May 21.5	July 1	....
- 9	90	83	none	6.0	11.7	0.0	May 16	June 19.5	....
-10	87	70	none	?	23.7	0.0	May 16	June 26	....
-11	90	61	none	?	16.3	0.0	May 25	July 14.5	....
-12	87	94	D-1	8.0	38.7	...	May 10.5	June 28.5	....
-13	64	89	28	3.0	16.3	0.3	May 24.5	July 3.5	Sep. 21
-14	80	95	none	1.0	19.0	0.0	May 30	July 3.5	....
-15	82	79	36	8.0	30.7	1.7	May 28.5	June 28.5	Sep. 14
-16*	84	82	26	3.0	18.7	0.3	May 14	July 7.5	Sep. 8
-17*	88	94	D-3	16.0	48.0	0.0	May 14	July 2	....
-18	72	86	45	6.5	18.7	1.7	May 28.5	June 30.5	Sep. 16.5
-19*	60	78	D-2	6.0	19.7	0	May 21	July 3	....
-20*	50	72	none	7.5	57.7	0.0	May 30	June 23.5	....
-21	80	81	44	3.5	11.3	1.0	June 6	July 13	Sep. 19
-22	69 (D-3)	D	25	0.0	....	0.7	....	D	Oct. 1
-24	84	97	D-3	5.5	49.0	0.0	May 27	June 20.5	....
-25*	76	80	40	0.5	37.3	3.0	May 26	July 2.5	Sep. 23.7
-26*	98	93	44	4.0	44.7	4.7	May 30	June 29.5	Sep. 16
-27	72	79	D-2	7.5	30.0	0	May 28.5	July 4	....
-28	82	83	56	12.5	15.0	1.0	May 18	July 10	Sep. 25
-29	72	50	30	5.0	5.7	0.7	May 18	July 5.5	Sep. 19.5
-30*	90	78	D-2	5.0	20.3	0	May 10	June 26	....
-31	62	82	18	3.5	26.3	1.0	May 20.5	July 2	Sep. 21
Total...	29	28	12	27	28	24	28	28	12
Means..	79.6	82.4	34.3	7.21	28.32	0.70	May 16.8	June 30.4	Sep. 20.3
	±2.27	±2.08	±3.35	±1.08	±2.54	±0.23	±2.49	±1.23	±1.81

*Plants illustrated in figure 16.

TABLE 11

REACTIONS IN THE ASPEN VALLEY POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
3969- 1*.....	47	39	39	5.0	7.0	2.0	May 25	June 27.5	Aug. 30
- 2.....	58	66	none	3.3	4.3	0.0	June 5	July 5.5	....
- 3.....	71	51	23	8.0	13.3	1.7	June 6.5	June 27.5	Sep. 14
- 4.....	44	52	25	2.3	10.7	2.3	June 6	June 25	Aug. 28
- 5.....	56	46 (D-2)	20	2.7	5	0.7	June 23.5	June 20	I
- 6.....	41	39 (D-3)	29	13.7	19.5	5.3	June 23	June 13	Sep. 1
- 7.....	65	43	25	4.0	3.7	2.3	....	June 24.5	Sep. 9
- 8.....	none	46	31	0.0	8.3	2.7	....	June 20	Sep. 12
- 9.....	41	43	14	5.0	10.0	1.3	June 3	June 30	Aug. 30
-10.....	37	55	34	0.7	5.0	3.3	June 26	July 7	Sep. 10
-11.....	56	63	33	4.0	10.7	2.3	June 1	June 29	Sep. 2.5
-12.....	none	76	D-1	0.0	3.3	...	....	June 30.5	....
-13.....	35	55	34	1.7	20.7	2.3	June 16	June 17.5	Sep. 6.5
-14*.....	54	68	26	12.7	49.3	0.7	June 7.3	June 27.5	Sep. 14
-15.....	15	41	23	0.3	10.0	1.7	June 5	June 24.5	Sep. 3.5
-16.....	72	47	D-1	3.0	17.3	...	June 5	June 16.5	....
-17.....	50	53	31	8.0	32.7	1.3	May 21.5	June 14	Sep. 4
-18.....	49	62	15	0.7	16.3	0.3	May 15	June 16	Sep. 4
-19.....	29	75	D-1	1.0	14.0	..	June 9	June 29.5	....
-20*.....	37 (D-2)	63	40	12	31.7	2.7	June 10	June 20.5	Sep. 4.5
-21*.....	34 (D-3)	64	D-1	0.5	18.7	...	....	July 9	....
-22*.....	55	81	34	5.3	40.7	3.0	June 12	June 28	Sep. 13
-23.....	49	47	5 (D-3)	1.3	11.3	0.5	June 9.5	June 21	Oct. 2
-24*.....	63	73	10	4.7	40.0	0.3	June 11.5	July 6.5	Oct. 11
-25*.....	46	61	21	2.3	20.7	1.0	June 11	July 2.5	Sep. 13
-26.....	49	57	24 (D-3)	10.7	35.0	0.5	May 18	June 16.5	Aug. 23
-27.....	52	60	22	2.7	3.3	2.7	May 25.5	June 24	Sep. 7.5
-28.....	36	77	none	1.0	14.3	0.0	....	July 10.5	I
-29.....	46	45	none	4.0	8.3	0.0	June 8	July 3.5	I
-30.....	40	55	D-3	6.0	7.7	0.0	May 17.5	July 5	....
Total........	28	30	22	30	30	26	25	30	21
Means.......	47.4	56.8	25.3	4.22	16.43	1.57	June 5.4	June 26.4	Sep. 8.5
	±2.40	±2.22	±1.93	±0.71	±2.28	±0.26	±2.24	±1.41	±2.44

*Plants illustrated in figure 17.
I=Flowering stems immature.

TABLE 12

REACTIONS IN THE YOSEMITE CREEK POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
3970- 1	52	49	24	10.3	2.0	0.3	May 27.5	June 12.5	Sep. 11.0
- 2	67	58	30	3.0	10.3	1.3	May 17.5	June 29.5	Sep. 4.5
- 3†	59	52	15	9.3	3.7	1.3	May 31.5	June 27	Sep. 12
- 4	68	65	none	8.0	28	0.0	May 14.5	June 10	I
- 5	36	42 (D-3)	13	12.7	5.5	0.7	May 14	June 10	....
- 6†	61	D	26	6.7	....	0.7	June 1	....	Sep. 1.5
- 7	31	52 (D-2)	D-3	9.3	13	0.0	May 2.5	June 10	....
- 8	16	46	34	1.0	1.3	2.7	May 19	June 10	Aug. 30.5
- 9†	47	65	25	13.7	16.7	3.3	May 10	June 17	Aug. 31.5
-10	25	48	35	3.0	16.0	7.3	May 24	June 12	Aug. 27
-11	64	56	29	15.3	9.7	4.7	May 18.5	June 15	Aug. 28
-12†	43	57	38	7.0	9.7	4.0	May 26.5	June 19.5	Aug. 28
-13†	32	57	36	2.7	12.0	7.0	May 8.5	June 20	Aug. 26
-14	47	62	23	4.0	11.0	0.7	June 7	June 17.5	Sep. 4
-15	14	62	40	0.3	24.0	6.3	June 16	July 7.5	Aug. 21
-16	53	63	37	10.0	7.3	3.0	May 15.5	June 21	Sep. 3.5
-17	42	53	35	6.3	21.7	7.0	May 19	June 17.5	Sep. 4.5
-18†	52	57	20	10.7	23.7	1.7	May 21.5	June 14	Sep. 2.5
-19	57	64	36	28.3	44.3	6.0	May 7.5	June 11.5	Sep. 1
-20	32	45	21	6.3	25.7	8.0	May 17	June 19.5	Sep. 1.5
-21	44	60	30	1.7	21.0	6.3	May 7	June 16	Aug. 29.5
-22	44	65	28	3.0	13.3	2.7	May 31	June 18.5	Aug. 29
-23	27	58	37	1.7	12.7	7.0	June 16	June 13	Aug. 25.5
-24	47	84	23	4.3	20.0	0.7	May 30.5	June 19.5	Sep. 13.5
-25	49	59	37	6.0	15.7	2.3	June 9.5	June 30.5	Aug. 31.5
-26	29	61	32	1.0	16.7	3.3	June 15	June 18	Aug. 30
-27	47	45	45	0.3	7.0	12.0	June 14	June 19.5	Sep. 6
-28	none	58	none	0.0	4.0	0.0	....	June 19.5	....
-29	26	53	40	1.3	14.7	4.3	June 16	June 16.5	Aug. 30.5
-30†	24	33	24	4.7	4.7	1.3	Apr. 30	June 13	Sep. 6
Total...	29	29	27	30	29	30	29	29	26
Means..	42.6	56.2	30.1	6.40	14.32	3.53	May 24.3	June 17.7	Sep. 1.4
	±2.66	±1.76	±1.55	±1.08	±1.73	±0.54	±2.64	±1.21	±1.09

†Plants illustrated in figure 7.
I =Flowering stems immature.

TABLE 13

REACTIONS IN THE TENAYA LAKE POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
3971- 1..	35	D-1	34	7.0	....	4.3	May 3.5	....	Aug. 21.0
- 2..	44	33	32	5.3	2.3	3.0	May 9	June 6.5	Aug. 19
- 3..	43	23	31	11.7	0.7	2.3	May 24.5	June 5	Aug. 27.5
- 4*	52	25 (D-3)	46	4.3	1.0	3.0	May 5	June 5	Aug. 22
- 5†	42	33	35	2.3	2.0	1.3	June 8.5	June 5	Aug. 26
- 6*	38	29 (D-3)	30	37.7	5.5	6.7	Apr. 24	June 18	Aug. 23
- 7..	31	21 (D-2)	31	15.3	11	3.3	Apr. 30	June 5	Aug. 19.7
- 8..	43	46	45	15.7	4.7	2.7	Apr. 17.5	June 5	Aug. 18.5
- 9*	31	32	36	0.3	1.7	2.3	....	June 17.5	Aug. 25
-10..	37	18	35	11.3	0.7	3.3	Apr. 26	June 11.5	Aug. 14
-11†	33	36	36	3.7	3.7	5.0	May 15.5	June 11.5	Aug. 19
-12..	12	24	19	0.7	2.0	3.7	May 4	June 5	Aug. 19
-13*	44	33	30	17.7	11.7	4.0	May 1.5	June 18	Aug. 17
-14..	29	40	40	0.7	9.0	9.3	May 25	June 15.5	Aug. 15.3
-15..	37	33	32	10.0	5.0	6.3	May 2	June 8.5	Aug. 16.7
-16*†	21	24 (D-3)	30	3.0	3.0	2.3	May 13.5	June 10	Aug. 14.5
-17..	44	52	36	14.0	13.3	3.7	May 3	June 14.5	Aug. 23.7
-18..	29	30	45	7.3	9.0	3.0	May 9.5	June 5.5	Aug. 20
-19..	25	28 (D-3)	24	4.3	0.5	4.3	May 4	June 5	Aug. 18
-20†	28	48 (D-3)	38	8.7	22.0	7.3	Apr. 26	June 28	Aug. 29.3
-21†	20	31	29	0.7	4.0	1.7	June 12.5	June 5	Aug. 19.5
-22..	29	34	29	7.3	4.3	3.3	May 10	June 3.5	Aug. 20.5
-23*	44	36	38	7.0	8.3	9.3	June 16	June 21	Aug. 28.5
-24*	40	43	32	7.0	8.7	4.3	May 31	June 7	Aug. 20
-25†	32	39 (D-3)	35	11.3	2.5	7.7	Apr. 27	June 15	Aug. 18.7
-26†	45	32 (D-3)	38	7.3	3.0	5.7	May 5	June 10	Aug. 25.7
-27..	22	33	D	2.3	3.0	....	June 1	June 18	....
-28..	26	43	35	14.0	21.0	11.0	May 3	June 14.5	Aug. 25
-29..	36	41	21	9.3	22.7	6.7	June 1.5	June 10	Aug. 26.7
-30..	24	38	27	16.7	5.7	5.7	Apr. 27	June 10	Aug. 15
Total....	30	29	29	30	29	29	29	29	29
Means...	33.9	33.7	33.4	8.80	6.62	4.71	May 11.4	June 10.8	Aug. 20.9
	±1.70	±1.52	±1.18	±1.38	±1.19	±0.45	±2.99	±1.14	±0.81

†Plants illustrated in figure 7.
*Plants illustrated in figure 18.

TABLE 14

REACTIONS IN THE TUOLUMNE MEADOWS POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
3972- 1	29	31	16	12.7	7.3	1.3	May 20.5	June 10	Aug. 13
- 2	29	24 (D-2)	D-1	1.0	4	....	May 27	June 10	....
- 3	18	D-1	D-1	1.3	....	....	May 23.5	....	....
- 4	20	19 (D-3)	21	2.3	3.0	3.3	May 2.5	June 10	Aug. 19.5
- 5	37	36 (D-3)	32	3.3	8.0	2.0	May 22.5	June 10	Aug. 17.5
- 6	20	28 (D-3)	36	1.7	4.5	5.3	May 2.5	June 17	Aug. 17.5
- 7	27	33	29	5.3	7.3	4.7	May 5	June 17.5	Aug. 21.5
- 8	28	30 (D-3)	32	1.0	7.0	1.7	June 13	June 20	Aug. 17.5
- 9	9	20	21	1.0	1.7	10.0	Apr. 25	June 10	Aug. 15.7
-10	18	29	34	2.0	5.7	3.0	Apr. 20	June 10	Aug. 19.3
-11	18	26	28	4.0	13.0	8.0	May 5	June 22.5	Aug. 14.0
-12	14	27	35	2.3	5.3	13.7	Apr. 30	June 5	Aug. 19.5
-13	41	42	31	10.3	21.3	4.0	May 11	June 11.5	Aug. 21.0
-14	29	32 (D-2)	28	3.0	4	2.3	May 17.5	June 10	Aug. 21.0
-15	none	29 (D-3)	39	0.0	5.5	10.7	....	June 15	Aug. 19
-16	25	39	31	3.0	7.0	0.7	May 3	June 10.5	Aug. 18
-17	15	36	23	2.0	18.3	0.7	June 10	June 12.5	Aug. 12
-18	34	42	32	1.7	14.7	6.3	July 2	June 7.5	Aug. 16.7
-19	19	39 (D-2)	29	1.3	30	1.7	July 8 5	June 20	Aug. 20.5
-20	40	43 (D-2)	26	14.0	58	8.0	Apr. 23	June 10	Aug. 15
-21	none	31	29	0.0	2.0	6.0	....	June 10.5	Aug. 14
-22	18	45 (D-3)	38	3.3	14.5	6.7	May 1	June 15	Aug. 18.7
-23	18	26	19	1.7	6.0	1.7	May 1	June 17	Aug. 22
-24	31	35	26	17.3	42.0	11.0	Apr. 22	June 11	Aug. 15
-25	32	39	28	3.0	39.3	18.3	May 25.5	June 12	Aug. 22.3
-26	20	29	18	5.3	10.3	1.0	May 30	June 19	Aug. 17
-27	none	39	33	0.0	5.7	5.3	....	June 18	Aug. 19
-28	25	20	19	2.3	1.0	3.7	May 18.5	June 22	Aug. 17.5
-29	22	43 (D-3)	31	8.7	19.0	17.3	Apr. 21	June 15	Aug. 22
-30	25	36	32	5.7	1.3	6.3	May 3	June 19	Aug. 18
Total...	27	29	28	30	29	28	27	29	28
Means..	24.5	32.7	28.4	4.02	12.65	5.88	May 14.7	June 13.7	Aug. 17.8
	±1.55	±1.39	±1.18	±0.79	±2.55	±0.91	±4.06	±0.87	±0.51

TABLE 15

REACTIONS IN THE TIMBERLINE POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather*	Timberline
3780- 1	36	34 (D-3)	34	0.8	1.0	1.7	June 16	June 5	Aug. 20
- 2	none	23 (D-2)	24	0.0	1	1.0	....	June 5	Aug. 28.5
- 3	32	D-1	24	3.0	....	1.0	May 19	....	Aug. 11
- 4	24	D-1	30	5.0	....	3.0	Apr. 26	....	Aug. 24.5
- 5	13	22 (D-2)	19	9.5	5	1.7	May 19	June 6	Aug. 17
- 6	13	18 (D-2)	22	5.0	3	4.0	May 5	June 15	Aug. 19.3
- 7	18	D-1	15	2.5	....	1.7	Apr. 13	....	Aug. 13
- 8	9	D-2	18	0.3	0	3.3	May 9	....	Aug. 11
- 9	28	29	21	12.0	3.7	2.3	May 4	June 14.0	Aug. 17
-10	21	D-2	27	5.3	0	4.7	May 10	....	Aug. 12.7
-11	6	26 (D-2)	24	0.3	9	4.3	May 5	June 10	Aug. 24
-12	14	39 (D-2)	20	4.0	17	3.7	May 31	June 10	Aug. 22
-13	19	28	10	4.0	2	0.3	May 26	June 10	Aug. 20
-14	16	40 (D-2)	36	0.5	16	6.7	Apr. 30	June 10	Aug. 19.5
-16	15 (D-3)	D-1	D-1	0.5	....	...	May 30	....	....
-17	13	25	21	3.2	1.0	3.3	Apr. 19	June 10	Aug. 23
-18	32	43	20	11.7	10.3	2.0	Apr. 10	June 10	Aug. 21
-19	32	36 (D-3)	29	7.7	8.0	2.7	May 17	June 10	Aug. 19
-20	20	43 (D-3)	27	2.7	16.0	4.3	May 5	June 10	Aug. 30
-21	32	none	25	3.5	0.0	1.0	May 16	....	Aug. 20.5
-22	29	D-1	29	8.0	....	4.7	May 8	....	Aug. 16.3
-23	28	32 (D-3)	27	5.5	4.5	2.0	May 24	June 10	Aug. 23.7
-24	29	30 (D-3)	22	0.3	6.5	1.3	May 23	June 10	Aug. 14
-25	19	27	23	1.3	2.7	1.0	May 6	June 5.0	Aug. 13
-26	24	27 (D-3)	30	1.0	1.0	0.7	May 27	June 10	Aug. 17
-28	17	40 (D-3)	16	0.3	4	0.3	May 20	June 10	Aug. 11
-29	19	36 (D-2)	20	1.0	29	1.0	May 23	June 10	Aug. 13
-30	15	34 (D-3)	27	0.3	1.5	2.7	May 19	June 10	Aug. 15.5
Total...	27	20	27	28	23	27	27	20	27
Means..	21.2	31.6	23.7	3.54	6.18	2.47	May 12.6	June 9.7	Aug. 18.4
	±1.55	±1.63	±1.09	±0.65	±1.54	±0.31	±2.97		±0.99

*Dates largely estimated from observations made in early August 1943, the only year the plants flowered.

TABLE 16

REACTIONS IN THE BIG HORN LAKE POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather†	Timberline
3780-101	none	none	16	0.0	0.0	2.3	....	....	Aug. 19
-102	15	26 (D-2)	20	12.3	10	1.7	Apr. 5	June 6	Aug. 13.5
-103	17	28 (D-2)	D	9.7	14	....	Apr. 14	June 5	....
-104*	10	none	22	1.3	0.0	5.3	Apr. 16	....	Aug. 14
-105	15	D-1	23	0.7	....	3.3	Apr. 26	....	Aug. 10.5
-106*	none	20 (D-2)	25	0.0	0.5	5.7	....	June 5	Aug. 12
-107*	12	5	27	1.3	0.3	2.7	May 27	....	Aug. 15.5
-108*	17	25	27	1.7	2.0	6.0	May 2	June 10	Aug. 11.7
-109*	18	11	28	2.3	1.0	4.0	Apr. 19	June 5	Aug. 13.5
-110*	9	none	25	0.7	0.0	3.3	....	....	Aug. 11.5
-111	21 (D-3)	17 (D-2)	16	1.0	6	2.7	May 6	June 5	Aug. 25
-112*	20	24	31	3.3	2.7	4.0	May 31	June 5	Aug. 12.5
Total....	10	8	11	12	11	11	9	7	11 ·
Means...	15.4	19.5	23.6	2.86	3.32	3.73	Apr. 29.6	June 5.9	Aug. 14.4
	±1.28	±2.86	±1.45	±1.15	±1.40	±0.42	±2.03		±1.25

*Plants illustrated in figure 19.

†Dates largely estimated from observations made in early August 1943.

TABLE 17

REACTIONS IN THE DANISH COASTAL POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS	
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather
2442- 1........	45	41	D-3	10.7	35.7	0.0	Apr. 22.5	July 9.7
- 2........	35	40	none	36.7	54.0	0.0	Apr. 28	July 2.3
- 3........	44	46	none	18.0	31.3	0.0	May 21	July 2.7
- 4........	55	38 (D-2)	none	6.0	30	0.0	May 26	July 10
- 5........	36	50 (D-2)	none	7.3	83	0.0	June 11	July 11
- 6........	53	54 (D-3)	none	33.0	36.5	0.0	May 29	July 10
- 7........	35	41 (D-2)	none	15.7	17.0	0.0	May 24	July 15
- 8........	39	43 (D-2)	D-3	42.0	27.0	0.0	May 30	July 15
- 9........	42	41 (D-2)	D-3	36.0	39.0	0.0	Apr. 19.5	July 1
-10........	47	56 (D-2)	D-3	34.0	54.0	0.0	May 12.5	July 10
-11........	32	28 (D-2)	D-3	61.5	11.0	0.0	May 4.5	July 1
Total..........	11	11	....	11	11	11	11	11
Means.........	42.1	43.5	....	27.36	38.05	0.00	May 15.4	July 7.9
	±2.28	±2.42		±5.23	±6.00		±5.13	±1.63

same holds true with regard to the number of stems. The longest stem grown is thought to be a better indicator of performance than the mean for a period of years, because the larger races of *Achillea,* quickly depleting the soil, decrease in size.

TABLE 18

REACTIONS IN THE LAPLAND POPULATION

PLANT NO.	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS	
	Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather
3766- 1...	44	38 (D-2)	none	19.7	2	0.0	Apr. 14.5	July 18
- 2...	48	47 (D-2)	none	28.3	14	0.0	Apr. 12.5	July 1
- 3...	33	21 (D-2)	D-3	19.5	1	0.0	May 28	July 15
- 4...	41	45 (D-2)	none	29.0	24	0.0	Apr. 15.5	June 20
- 5...	44	42 (D-2)	D-3	23.0	40	0.0	Apr. 7	June 20
- 6...	28	25 (D-2)	D-2	8.3	9	0.0	May 6	July 1
- 7...	24	52 (D-2)	7	4.5	37	0.0	May 28	June 20
- 8...	none	12 (D-2)	none	0.0	1	0.0	....	July 15
- 9...	34	37 (D-2)	D-3	11.7	40	0.0	Apr. 17	June 20
-10...	46	D	D-3	48.7	..	0.0	Apr. 25	....
-11...	46	38 (D-2)	D-3	23.3	48	0.0	Apr. 20.5	June 20
-12...	57	59 (D-2)	none	44.7	90	0.0	Apr. 7	June 20
-13...	32	42 (D-2)	none	9.7	31	0.0	Apr. 26	June 20
-14...	39	D	none	19.3	..	0.0	Apr. 15.5	....
-15...	38	44 (D-2)	none	8.0	20	0.0	May 11	June 20
-16...	23	31 (D-2)	none	12.0	15	0.0	May 19	June 20..
-17...	32	43 (D-2)	8	14.0	46	0.3	Apr. 27.5	June 15
-18...	20	25	none	0.7	16.0	0.0	June 8	June 30
-19...	24	29	none	11.7	8.5	0.0	Apr. 19	June 24
-20...	30	33 (D-3)	none	3.5	3.0	0.0	May 21	June 21
Total.....	19	18	2	20	18	20	19	18
Means....	36.0	36.8	7.5	16.98	24.75	0.00	Apr. 29.9	June 26.0
	±2.30	±2.65		±2.97	±5.37		±4.34	±2.39

Under the extreme conditions at Timberline, the coastal races were almost eliminated after the first winter, and none flowered. Only 4 of the 61 individuals from Bodega and San Gregorio survived the second winter; only 1 plant, 3777-21, was still alive after four winters, and it was then a diminutive, dying rosette. It is evident that these plants cannot synthesize enough food material during the brief growing season at Timberline to survive during the long period of enforced dormancy. Some individuals may persist for a short period of years with the aid of the food reserves on hand at the time they were transplanted.

TABLE 19

SUMMARY OF REACTIONS IN RACES OF ACHILLEA

CULTURE NO.	ORIGIN	LONGEST STEMS (CM.)			NUMBER OF STEMS			DATE OF FIRST FLOWERS		
		Stanford	Mather	Timberline	Stanford	Mather	Timberline	Stanford	Mather	Timberline
3776....	Bodega	48.9±1.98	30.8±1.78	....	19.27±1.64	18.19±2.74	0.00	May 21.1±2.15	July 11.5±1.67	....
3777....	San Gregorio	98.0±3.14	59.5±2.49	....	30.90±2.73	19.89±2.26	0.00	May 7.8±1.73	July 10.7±1.42	....
3965....	Clayton	70.0±1.57	37.3±1.99	....	16.08±1.24	7.51±1.05	0.00	Apr. 12.8±1.38	June 16.8±1.73	....
3966....	Knights Ferry	79.4±2.40	36.6±1.74	....	24.98±1.62	8.63±1.15	0.00	Apr. 15.7±1.71	June 14.7±1.23	....
3967....	Groveland	83.6±2.12	58.2±2.03	15.5±2.36	15.75±1.27	22.81±2.84	0.65±0.19	May 13.8±1.88	June 26.2±1.00	Sep. 16.5±1.76
3778....	Mather	79.6±2.27	82.4±2.08	34.3±3.35	7.21±1.08	28.32±2.54	0.70±0.23	May 16.8±2.49	June 30.4±1.23	Sep. 20.3±1.81
3969....	Aspen Valley	47.4±2.40	56.8±2.22	25.3±1.93	4.22±0.71	16.43±2.28	1.57±0.26	June 5.4±2.24	June 26.4±1.41	Sep. 8.5±2.44
3970....	Yosemite Creek	42.6±2.66	56.2±1.76	30.1±1.55	6.40±1.08	14.32±1.73	3.53±0.54	May 24.3±2.64	June 17.7±1.21	Sep. 1.4±1.09
3971....	Tenaya Lake	33.9±1.70	33.7±1.52	33.4±1.18	8.80±1.38	6.62±1.19	4.71±0.45	May 11.4±2.99	June 10.8±1.14	Aug. 20.9±0.81
3972....	Tuolumne Meadows	24.5±1.55	32.7±1.39	28.4±1.18	4.02±0.79	12.65±2.55	5.88±0.91	May 14.7±4.06	June 13.7±0.87	Aug. 17.8±0.51
3780....	Timberline	21.2±1.55	31.6±1.63	23.7±1.09	3.54±0.65	6.18±1.54	2.47±0.31	May 12.6±2.97	June 9.7	Aug. 18.4±0.99
3780....	Big Horn Lake	15.4±1.28	19.5±2.86	23.6±1.45	2.86±1.15	3.32±1.40	3.73±0.42	Apr. 29.6±2.03	June 5.9	Aug. 14.4±1.25
2442....	Denmark	42.1±2.28	43.5±2.42	....	27.36±5.23	38.05±6.00	0.00	May 15.4±5.13	July 7.9±1.63	....
3766....	Lapland	36.0±2.30	36.8±2.65	7.5	16.98±2.97	24.75±5.37	0.00	Apr. 29.9±4.34	June 26.0±2.39	....

INDIVIDUAL DIFFERENCES IN RESPONSE. Basic to theories of natural selection is the question whether some individuals of a wild population have a greater capacity than others to survive in new environments. It is obvious that none of the plants from the coast had a chance to persist at Timberline, but some of them grew fairly well at Mather. Even after discounting differences due to injuries or minor inequalities of handling, it is clear that in each population the individuals differed considerably in their reactions to the Mather environment. A study of tables 5 and 6 will make this evident.

Considering length and number of stems as a fair measure of vigor in any one environment, certain plants in tables 5 and 6 stand out as extremes in trends of reaction. Such extreme variants show the evolutionary possibilities of populations. Even though every one of the 61 individuals in the two populations has shorter stems at Mather than at Stanford, some are relatively much shorter, but in these a large increase in number of stems may more than compensate for the decreased length. The means of the two populations show a great reduction in length and a rather small reduction in number of stems at Mather, but individual plants, evolutionarily the most interesting, deviate markedly from the means.

Examples of four kinds of deviating plants included in tables 5 and 6 are singled out for comparison in table 20. One plant of each kind has been selected from each coastal population. The four groups are: (1) those vigorous at both Stanford and Mather; (2) those vigorous at Stanford but weak at Mather; (3) those relatively weak at Stanford but vigorous at Mather; and (4) those weak in both environments. The differences in reaction are impressive, and could be augmented by other examples from the tables.

That variants differing so widely in their modes of reaction can be selected from samples as small as 60 individuals suggests significant evolutionary possibilities. The less specialized fraction, represented by the plants of group 1, possesses a wide adaptability to different environments. Variants of group 2 are exceptionally robust types of the class to which the majority of the coastal plants belong, thriving best in the lowland or coastal environment. Those of group 3 produce many more stems in the mid-Sierran environment than in the Santa Clara Valley of the Coast Ranges. Plants of group 4, that are weak in both environments, would probably be eliminated under conditions of natural competition at either place, although some might prove to be extreme specialists which have been favored by a truly maritime habitat.

Such a system of individual variation as that found in these coastal

populations obviously enables plants to meet most of the contingencies that result from slowly changing environments. This system provides both a remarkable fitness for the climates in which these populations are native, and a flexibility, provided by the different capacities of the individual members, for succeeding in other environments. It is even conceivable that if the large tetraploid forms that now occupy middle altitudes in the Sierra Nevada were to disappear, forms of the hexaploid coastal populations able to populate those areas could arise through selec-

TABLE 20

COASTAL PLANTS WIDELY DIFFERENT IN THEIR REACTIONS

	STANFORD		MATHER	
	No. of stems	Height (cm.)	No. of stems	Height (cm.)
1. Vigorous at both stations:				
Bodega: 3776-3................................	34.0	67	39.0	53
San Gregorio: 3777-22.........................	36.0	108	24.3	71
2. Vigorous at Stanford, weak at Mather:				
Bodega: 3776-1................................	27.0	52	2.3	25
San Gregorio: 3777-12.........................	34.5	99	8.7	58
3. Relatively weak at Stanford, vigorous at Mather:				
Bodega: 3776-23...............................	7.0	40	47.0	35
San Gregorio: 3777-10.........................	26.5	83	43.3	74
4. Relatively weak at both Stanford and Mather:				
Bodega: 3776-8................................	3.5	37	9.0	20
San Gregorio: 3777-20.........................	13.5	70	6.7	44

tion. The adjustment to Sierran conditions of such a new ecotype, however, would not duplicate that of the present-day ecotype there.

Although marked reactional differences exist between individuals of the coastal populations, the principal features of the races they represent remain fairly constant. Lateness of flowering, continuation of growth during hot summer periods, and dense green foliage distinguish the coastal plants from those of the foothills.

One distinct variant, 3777-27 of the San Gregorio population, the second from the right in the lower row of figure 6 (p. 17), was interesting because morphologically it resembled the foothill form. The resemblance in morphological characters, however, was not extended to a similarity in reaction at the mountain stations, for from table 6 one can see that it flowered as late as the other plants of the coastal type, and unlike the

foothill form was not appreciably reduced in size at Mather. Further-more, during the summer, when plants of the foothill race were dormant, it remained green and active like a typical coastal plant.

DISTINCTNESS OF THE BODEGA AND SAN GREGORIO POPULATIONS. The similar capacity of these two coastal populations to survive in the Stanford and Mather climates has been emphasized. In chapter II the differences between the low, compact habit of the plants of the Bodega population, from an extreme maritime environment, and the taller plants of San Gregorio, from farther inland, were pointed out. The same relative differences in stature are observed at Mather as at Stanford, and are apparent from a study of stem length in tables 5 and 6; but the difference in time of flowering, appreciable at Stanford, is not evident at Mather. The densely crowded leaf segments of the Bodega form are also distinctive at Mather. In the more continental Mather climate the strictly maritime Bodega population seems to have been somewhat more weakened than the San Gregorio, for more of its plants died there.

THE CLAYTON AND KNIGHTS FERRY POPULATIONS

These forms from the dry interior foothill region of California are much less successful at the mountain stations than are the coastal populations. They, too, although normally winter-active, are forced into dormancy during the Mather winter. When they resume growth in early spring they also are weak, but, if not further weakened by late spring freezes, develop as quickly as at Stanford, producing stems before the rosette has grown large. But these stems are much fewer and shorter than those developed on the divisions at Stanford. At Mather, as at Stanford, the foothill forms flower approximately one month earlier than the coastal.

Following the rapid maturing of seed in July, the foothill plants adhere to their normal cycle and pass into a period of summer dormancy that is evidently hastened by the high day temperatures and intense solar radiation. The two periods of dormancy, one during the winter, and the other during the summer, make their growing season at Mather very much shorter than it is either in their native environment or at Stanford. There is therefore little opportunity for building the reserve food materials needed to carry them through their long periods of inactivity. The coastal races fare better at Mather chiefly because they continue to grow actively through the summer and fall.

The surviving plants of the Clayton and Knights Ferry populations in the Mather garden are small and weakened. Some are unable to produce

any flowering stems; many die after the second or third winter; and others die even sooner. At Timberline few plants survive even a single winter, and only 2 out of the original 60 lived through the second. Figure 14, constructed in the same way as figure 13, illustrates the reactions of 7 plants of the Knights Ferry population at the three stations. It shows the obvious reduction in size at Mather, and the lack of survival at Timberline. The individual on the extreme right, 3966-16, was too weak at Mather to advance beyond the rosette stage. The rather frequent deaths at Mather are exemplified by the third plant from the left, 3966-12. More complete data from all the plants of the Clayton and Knights Ferry populations are presented in tables 7 and 8, in which height, number of stems, and date of first flowers are tabulated for every plant at each of the transplant stations.

The close similarity of these two populations is apparent from a comparison of their means in table 19, a summary compiled from tables 5 to 18. The Knights Ferry population, however, is the more floriferous at Stanford. In characters other than those tabulated the similarity continues, and since the two forms are alike both morphologically and in their reactions, and come from the same climatic belt, they are regarded as members of the same climatic race, or ecotype, even though they are from opposite sides of the San Joaquin Valley.

The plants of the foothill ecotype are specialized to fit the climate of the interior Coast Range and foothill regions and are therefore less adapted to the Mather climate than are the less specialized coastal races. One individual, 3966-20 from Knights Ferry, illustrated in figure 14, was so exceptionally tall and vigorous at Stanford that it was noted for its resemblance to the tall coastal form, but even this plant conformed to the reaction pattern of the foothill race when transplanted, and was very much weakened at Mather. Physiological differences among the individuals of the foothill populations would probably have stood out better had these plants been tested under conditions halfway between those at Stanford and at Mather, for the very contrasting environments of these stations constitute too coarse a sieve to screen out differences within such a specialized race.

THE GROVELAND POPULATION

This form, from the Lower Transition life zone, comes from a climatically and floristically critical region where the arid grasslands and savannas of the Great Valley and foothills give way to heavy stands of coniferous forest in a moister region. In table 21 temperatures and precipitations
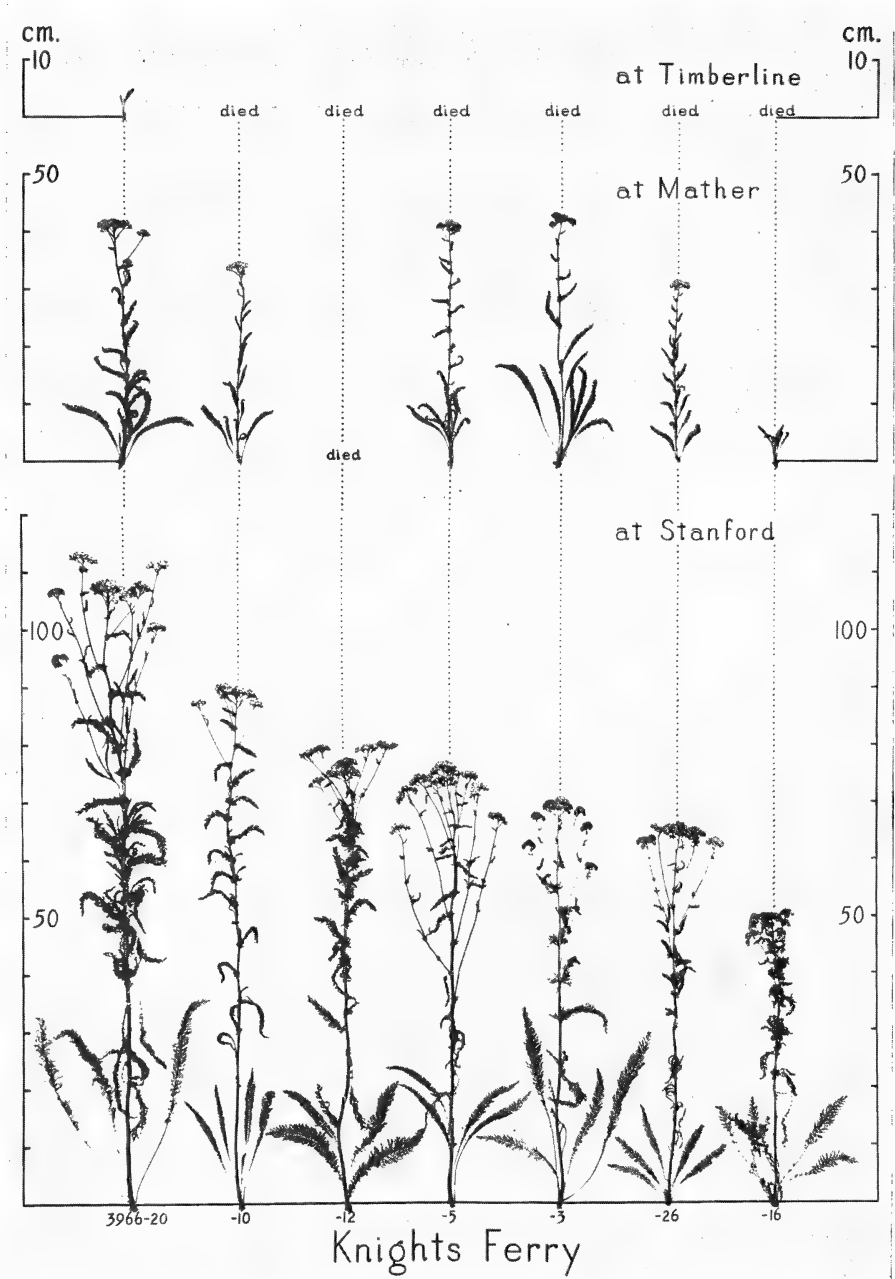
FIG. 14. Responses of clones of 7 plants of the Knights Ferry population from the interior foothill region (elevation 90 m.) at Stanford, Mather, and Timberline. The numbers at the bottom are those of the individual plants; their records may be traced further in table 8.

TABLE 21

COMPARISON OF TEMPERATURE AND PRECIPITATION AT FIVE STATIONS IN THE SIERRAN TRANSECT

	OAKDALE (ELEV. 65 M.)			GROVELAND (ELEV. 860 M.)			LAKE ELEANOR (ELEV. 1417 M.)			HUNTINGTON LAKE (ELEV. 2134 M.)			ELLERY LAKE (ELEV. 2890 M.)		
	Jan.	July	Ann. mean	Jan.	July	Ann. mean	Jan.	July	Ann. mean	Jan.	July	Ann. mean	Jan.	July	Ann. mean
Mean maximum temp. (°C.)......	10.89	35.44	23.44	10.28	31.55	19.88	8.33	29.83	18.21	5.67	23.39	13.33	1.73	20.0	9.71
Mean minimum temp. (°C.)......	1.06	14.01	7.21	0.39	13.11	5.60	-3.83	13.00	3.67	-8.11	9.17	0.01	-11.83	5.67	-3.94
Highest temp. (°C.)	21.7	45.6	36.29	21.7	38.9	30.79	23.9	38.3	30.83	20.6	31.1	26.76	15.6	28.3	20.5
Lowest temp. (°C.)	-6.7	8.3	-0.84	-12.8	2.8	-3.89	-21.7	0.0	-9.54	-27.8	0.0	-13.8	-31.7	-3.3	-18.4
Mean precipitation (cm.)..........	6.81	0.00	35.61	31.20	0.08	107.64	21.68	0.30	103.01	12.20	0.23	75.18	12.80	1.75	78.32

from United States Weather Bureau stations at Oakdale, Groveland, Lake Eleanor, Huntington Lake, and Ellery Lake are compared. Oakdale is located at the lower edge of the oak belt on the east side of the Great Valley, and the data from this locality give an impression of the temperature and moisture conditions under which the near-by Knights Ferry population grows. Groveland is not much colder than Oakdale, but it has three times the precipitation. As was explained in chapter II, the Lake Eleanor station corresponds to Mather, the Huntington Lake station to Aspen Valley, and Ellery Lake to Timberline.

The Groveland form, which is tetraploid, is much more vigorous at Mather than the hexaploid foothill forms, and some of its individuals have a slight ability to survive at Timberline. This can be seen by comparing the average number and length of stems produced at the three stations—fair measures of vigor—as shown in table 19. The Groveland population produced most stems at Mather, but the two populations of the foothill race were distinctly most vigorous at Stanford. The former was also able to produce a few stems at Timberline, where 15 plants survived the second winter, although these were reduced to 2 after the fourth winter. Only a few foothill plants survived even a single winter at Timberline. There were also significant differences in time of flowering, the Groveland population blooming a full month later at Stanford, and approximately ten days later at Mather. At Timberline the Groveland survivors flowered so late that they had no chance to ripen seed; also, they were so susceptible to frost injury that many stems were killed before they were able to flower.

Figure 15 illustrates the reactions of 7 individuals of the Groveland population at the three stations, and should be examined in connection with the other similarly constructed figures of the series (figs. 13–19). This population at Stanford performs similarly to the one from Knights Ferry, but it shows considerable improvement over that population at Mather and Timberline.

The Groveland plants, from 915 m. elevation, when brought into the garden at Mather at 1400 m. are subjected to a less drastic environmental change than either the coastal or the foothill races. Consequently, they fare better than the members of any of the preceding races, but they still do not attain the full vigor of the Mather natives.

Individual variation in this population can be observed in table 9 (p. 54), in which height, number of stems, and date of first flowers are tabulated as before. All plants except one were shorter at Mather than at Stanford, but their proportionate differences were not maintained in
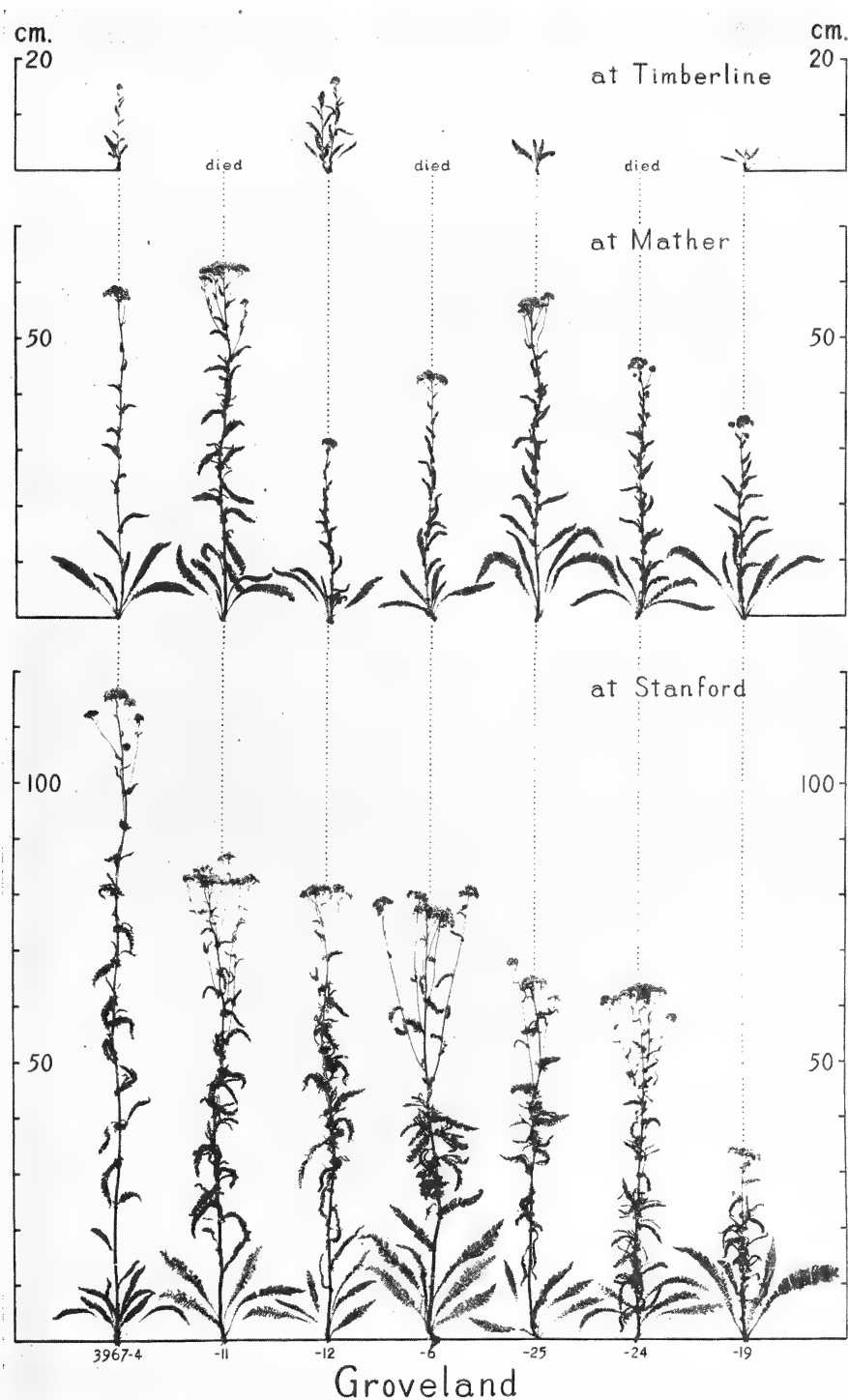
FIG. 15. Responses of clones of 7 plants of the Groveland population from the lower Sierra Nevada (elevation 915 m.) at Stanford, Mather, and Timberline. The numbers at the bottom are those of the individual plants; their records may be traced further in table 9.

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the reduced size. Some plants flowered most freely at Stanford, others at Mather, and still others were equally productive in both environments. Although the Groveland form is morphologically similar to the foothill plants, no plant from Groveland reacted like those from the foothills or the coast.

THE MATHER POPULATION

The climatic differences between Groveland and Mather are not large, and the altitudinal span between them is only 485 m., yet the races of *Achillea* in the two localities are significantly different. Two important climatic factors, temperature and precipitation, are compared in table 21, with the data from Lake Eleanor representing approximately the climate at Mather. The annual mean maximum and minimum temperatures are, respectively, only 1.67° and 1.93° C. lower at Lake Eleanor than at Groveland. The January minimum at Lake Eleanor, however, drops nearly 4° below freezing, whereas that at Groveland hovers around zero. This critical difference, reflected in a growing season 48 days longer at Groveland, is associated with the fact that Groveland Achilleas are winter-active at Stanford, whereas the majority of those from Mather are dormant.

The differences between the Groveland and Mather populations are most evident in the garden at Mather, where both attain full expression. Here the Mather form is significantly the taller and has more stems (table 19). At Timberline a larger percentage of the Mather plants survive, for 17 out of 29 lived through the fourth winter (table 10). Some of these attained considerable size, but their stems were usually killed by early frosts before they had a chance to flower, or they flowered too late to mature any seed. At Stanford, the Mather and Groveland populations are alike except for the important difference that approximately two-thirds of the Mather plants are winter-dormant. No recognizable morphological differences between the two populations have been observed at any of the stations, and there are no significant differences in earliness. Some of these observations can be visualized by a comparison of the sample of 7 individuals of the Mather population shown in figure 16 with the Groveland plants in figure 15.

Table 19 shows that the Mather native far outperforms any other race from the California transect in the Mather garden. The data in table 10 (p. 55) show that 9 of the 29 Mather plants are tallest at Stanford, 15 are tallest at Mather, and 5 are of approximately the same height at the two stations; all, however, produce more stems at Mather.

The most striking differences between individuals of the Mather popu-

cm.   at Timberline   cm.

50   50

died   died

100   at Mather   100

50   50

100   at Stanford   100

50   50

3778-26   -30   -17   -25   -16   -19   -20
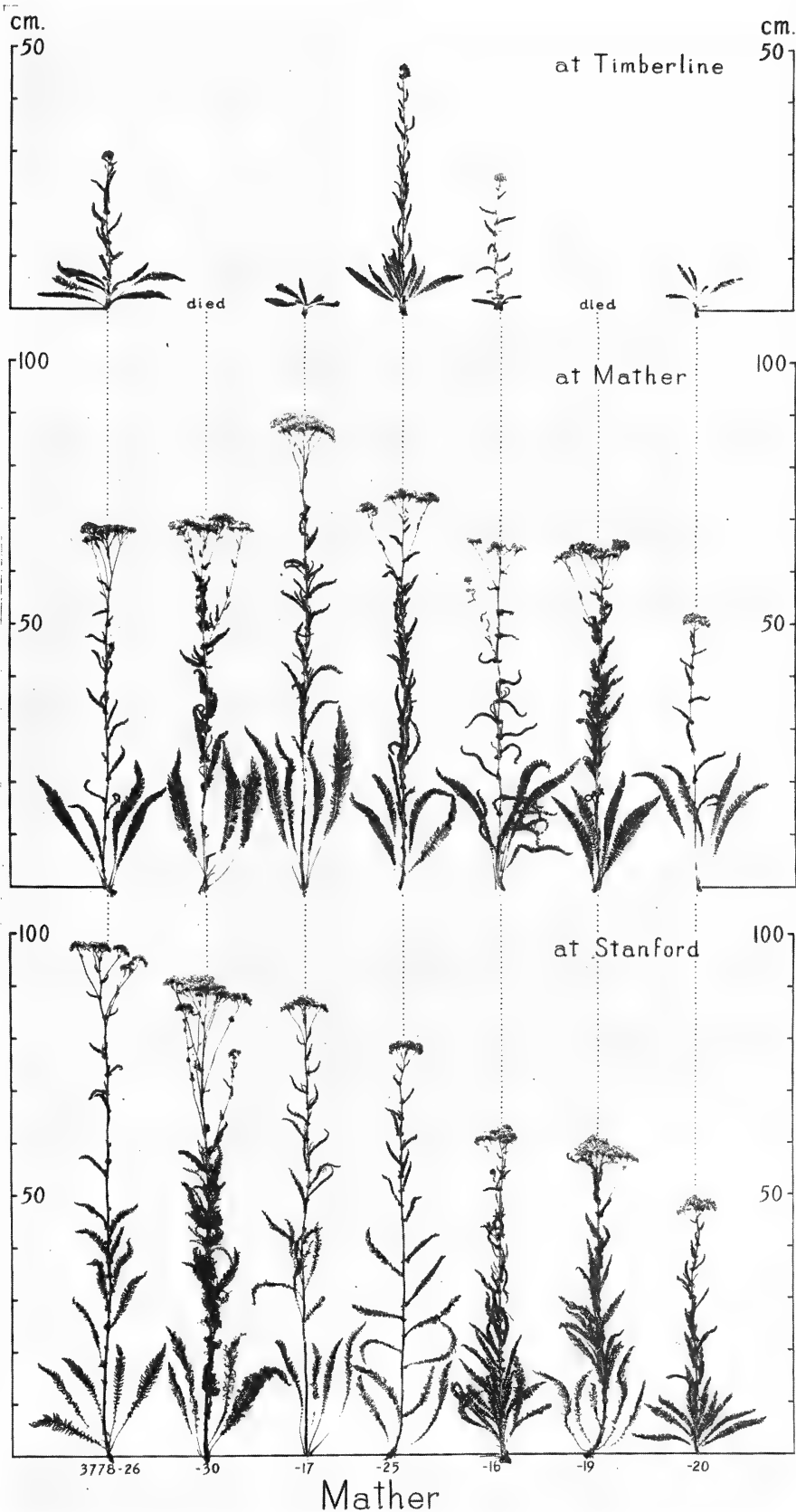
Mather

FIG. 16. Responses of clones of 7 plants of the Mather population from the central Sierra Nevada (elevation 1400 m.) at Stanford, Mather, and Timberline. The numbers at the bottom are those of the individual plants; their records may be traced further in table 10.

lation are seen at Timberline, where certain plants become as much as 56 cm. tall, others remain weak rosettes, and still others die soon after transplanting. Two of the tall plants, 3778-25 and -26, both of which are illustrated in figure 16, flowered all four years at Timberline, but always too late to ripen seed. One of them, 3778-25, was as resistant to frost injury as the native alpines, and was not injured by nightly minimum temperatures between $-4°$ and $-6°$ C. over a period of two weeks in September. Although seed was not ripened, the existence of frost-resistant individuals among a population with a preponderance of highly frost-susceptible individuals suggests evolutionary possibilities within the Mather race.

It is of interest to examine such a population for plants that may have reactional characteristics of the form from the next higher level. A few plants of the Mather population, for example 3778-19 and -20 (shown in figure 16) and -31, since they are short at Stanford, somewhat resemble typical plants from Aspen Valley, 550 m. higher in altitude. But a closer analysis of the records shows that at Stanford they flower earlier, and at Timberline they either die or flower later than the Aspen Valley plants; that they are more susceptible to frost injury; and that one of them, unlike any Aspen Valley plant, is somewhat winter-active at Stanford. Even though no individual in the Mather sample replicates the Aspen Valley type, it seems likely, when the potential recombinations of characters are considered, that new derivatives could be selected having the Aspen Valley attributes.

THE ASPEN VALLEY POPULATION

The differences between the Mather and the Aspen Valley populations at the three transplant stations are somewhat greater than those between the Groveland and Mather populations, but together the three form a well graded series.

A comparison of the temperatures and precipitation at Lake Eleanor with those at Huntington Lake, nearly 200 m. higher than Aspen Valley but farther south, gives some idea of the climatic differences between the natural habitats of the Mather and the Aspen Valley populations (table 21). Temperatures are appreciably cooler at Huntington Lake, the mean maxima and minima being approximately $3°$ to $5°$ C. lower. The average growing season, correspondingly, is some 31 days shorter, as shown by the curves in figure 4 (p. 14). The lower precipitation at Huntington Lake is doubtless more than compensated for by the lower rate of water loss due to lower temperatures. The larger winter snow pack and the reduced

rate of evaporation during the summer conserve moisture, making it available to most plants throughout their growing season.

The rather different flora at Aspen Valley, described in chapter II, indicates that plants are materially influenced by this much change in climate. The composition of the natural populations of *Achillea* strongly reflects such a selective influence. Figure 17, which shows 7 representative individuals, illustrates what happens when Achilleas from Aspen Valley are grown in the three climates of the transplant stations. The survival and development of this population at Timberline is very much improved over that of previous populations. Few plants, however, become fully mature there, and, since many are weak, the culture cannot be classified as truly successful. Furthermore, at the alpine station the herbage of approximately one-half of the survivors was observed to be yellowish green rather than dark green as at the other stations. Yet this population from an altitude of 1950 m. gives the first real promise of having individuals that might persist indefinitely in the alpine environment.

At Stanford the plants from Aspen Valley flower poorly and are the latest of all the populations. They are three weeks later than the Mather native, which came from an elevation 550 m. lower. They are delayed more than the lowland forms because of winter dormancy, and more than the higher-altitude forms because of slower acceleration in spring growth. This trend in earliness is reversed at Mather and Timberline, where the Aspen Valley form flowers distinctly earlier than the Mather (table 19, p. 63). The Aspen Valley form is most vigorous and floriferous at Mather and is also able to flower somewhat at Timberline, although the majority of plants rarely ripen seed there. From table 19 it can be seen that the Aspen Valley population is a step in a regular trend, in which populations from progressively higher altitudes become progressively earlier at the alpine station.

The full report on the performance of the 30 Aspen Valley transplants at the three stations is summarized in table 11 (p. 56). When the individual variability in reaction is studied, two individuals, 3969-3 and -16, might actually be mistaken for members of the Mather population. They either flower late or die at Timberline, and are much taller than the average at Stanford, but flower so late there that only one Mather plant is comparable. Another Aspen Valley plant, 3969-6, is comparable to plants from the Tenaya Lake population 550 m. higher up the mountains. Its stems are shorter than average at Stanford and Mather, but longer at Timberline. Its leaves are short and narrow in all environments, but they are green instead of gray-pubescent as in the *alpicola* form found at

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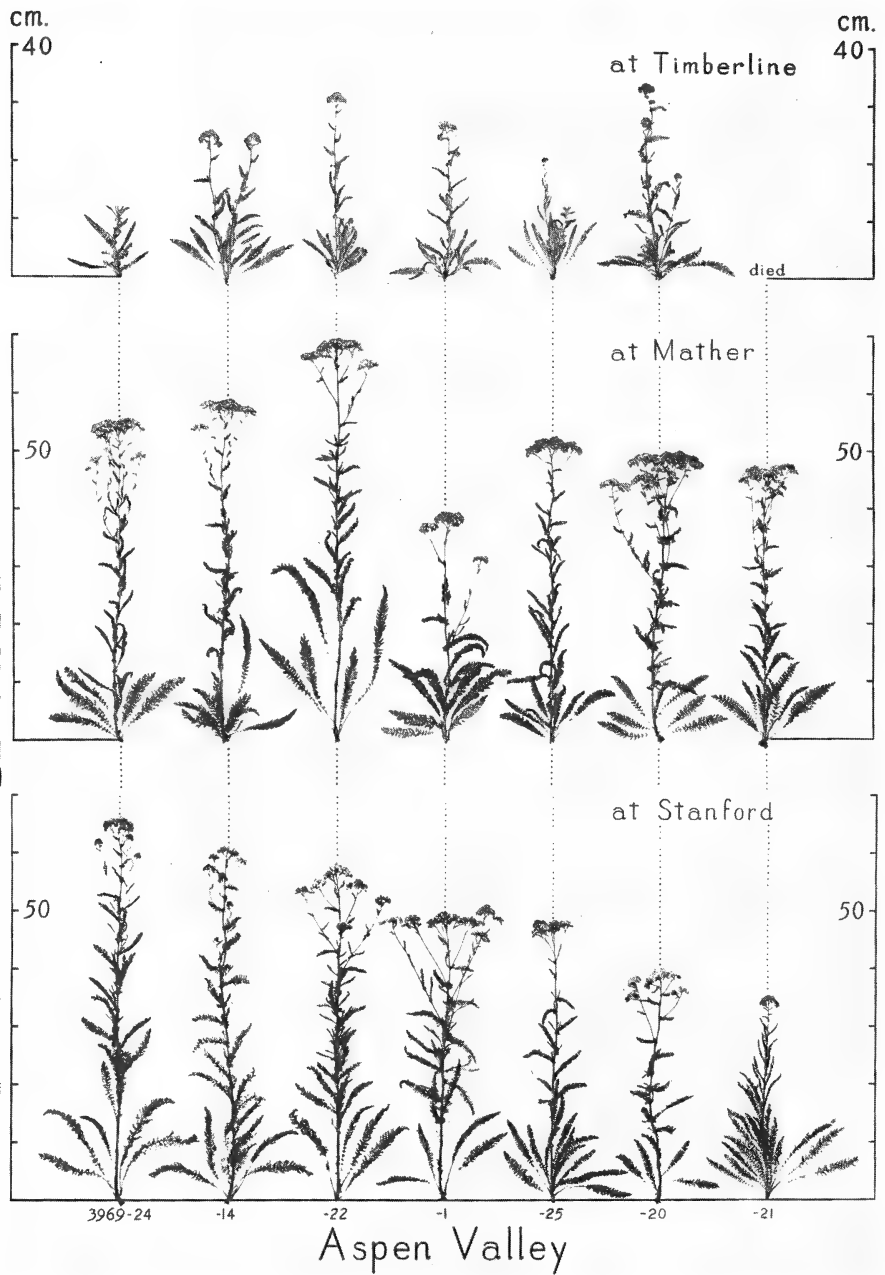
FIG. 17. Responses of clones of 7 plants of the Aspen Valley population from an upper middle altitude (1950 m.) of the Sierra Nevada at Stanford, Mather, and Timberline. The numbers at the bottom are those of the individual plants; their records may be traced further in table 11.

Tenaya Lake. This variant is also frost-resistant at Timberline, where it flowers early enough to mature seed in favorable years. Such a plant could doubtless succeed at Tenaya Lake.

Much variation in frost resistance at Timberline is observed in the Aspen Valley population. There are individuals as resistant as the alpines, others highly susceptible, and intermediates with every grade of ability to resist frost. Resistant and susceptible forms are found among both early- and late-flowering individuals, indicating recombinations of these characters. Frost resistance is of importance for survival at high altitudes because of the short growing season. Often late flowering and maturation of seed take place after frosty fall weather has set in. In the populations of *Achillea* from successively higher elevations one finds an increasing percentage of plants showing relatively high frost resistance.

The profound effects of modifications under different environments are well brought out by a comparison of the Groveland, Mather, and Aspen Valley populations in table 19. At Stanford the first two are very similar, but the winter-dormant Aspen Valley form, with shorter stems and leaves, appears to be markedly different. At Mather the Mather population dominates in all respects, standing out from both the others, which are much alike there. At Timberline, where the Mather population is intermediate, the Groveland and Aspen Valley forms contrast strongly, for the former is almost completely eliminated, whereas the latter survives with some degree of success.

THE YOSEMITE CREEK POPULATION

This population from 2200 m. elevation is a connecting link in the series between Aspen Valley at 1950 m. and Tenaya Lake at 2500 m. Its reactions at the three transplant gardens are rather similar to those of the Aspen Valley form. This becomes evident in the summary table 19 (p. 63). The slight statistical difference in the length of stems of the two at Timberline would disappear if the 1946 data were included in the computations, for the unusually long season that prevailed that year favored the growth of races from lower altitudes. There are significant differences in earliness of flowering between the Yosemite Creek and Aspen Valley populations, however, since the Yosemite Creek form flowers 8 to 13 days earlier at all the stations. At Stanford and Mather both populations have fairly wide green leaves, but at Timberline the Yosemite Creek plants become much grayer, so that they bear a strong resemblance to subalpine forms.

A detailed account of the performance of individual plants of the

Yosemite Creek population is presented in table 12 (p. 57). Variations in reaction patterns similar to those of other populations are noticeable here. For example, 3970-27 is very tall and has many stems at Timberline like true alpine forms, but its herbage is susceptible to frost injury like that of plants from lower altitudes. Another plant, 3970-30, which is illustrated at the extreme right of figure 7 (p. 27), has all the reactional and morphological characteristics of races from higher altitudes and might be mistaken for a native from Timberline at all three stations. By way of contrast, the plant 3970-19 far surpasses the others of the population in its production of flowering stems at the two lower stations. No plant, however, corresponding to any of the Mather population was found in the sample from Yosemite Creek.

The Yosemite Creek population survives very well at Timberline, for only one plant died during the four-year period, although approximately 65 per cent of the individuals had stems or inflorescences killed by frost. Because this population flowers so early, even some of the frost-susceptible plants are able to produce ripe seed in favorable years. A slight differential in the time of flowering, such as that between the Aspen Valley and Yosemite Creek populations, can be decisive in certain years.

When every aspect of the variation has been considered, the Aspen Valley and Yosemite Creek populations appear to be much alike in reaction, and therefore possibly belong to the same ecotype, although the population from the higher elevation is somewhat better adapted to higher altitudes.

THE TENAYA LAKE POPULATION

As one ascends from Yosemite Creek to Tenaya Lake the composition of the Sierran flora changes perceptibly, although species common to the two places are fairly numerous. A parallel change takes place in the composition of the *Achillea* populations. At Aspen Valley and Yosemite Creek the great majority of plants are of the *lanulosa typica* type, and only a small fraction have the narrow, gray leaves and slender stems of *lanulosa alpicola,* but at Tenaya Lake all fall into the *alpicola* category.

The morphological change is accompanied by a definite difference in the reactions of the plants at the transplant stations. As table 19 (p. 63) indicates, the Aspen Valley and Yosemite Creek populations are definitely tallest and produce the most stems at Mather, but plants of the Tenaya Lake population reach approximately the same size at all three stations. At Timberline the Tenaya Lake is among the tallest of all the populations in the garden, even surpassing in stature the Timberline

native. Since at this station the races from lower elevations in most years are much inhibited, and those from higher elevations are genetically short, none of the populations ordinarily exceed in stature the one from Tenaya Lake.

Compared with the population from Yosemite Creek, the one from Tenaya Lake is seven to thirteen days earlier in flowering at all stations and is definitely more frost-resistant. For example, observations made at Timberline during an extended period of frosty weather during 1946 disclosed that among the Tenaya Lake plants, 79 per cent had undamaged inflorescences, as compared with 35 per cent from Yosemite Creek. Most of the plants from Tenaya Lake are able to produce ripe seed at Timberline nearly every year.

The reactions of 7 plants chosen to represent the range of variation in the population are illustrated in figure 18. The poor performance of some individuals at Mather is in contrast with their relatively vigorous development at Timberline and Stanford. The Achilleas from higher altitudes are more shallow-rooted than those from middle elevations, and consequently at Mather during the summer they suffer from lack of moisture in the light-textured, black soil, which becomes hot and dry near the surface but remains moist below.

The plant-by-plant record is given in table 13 (p. 58). Reactional differences among individuals can be detected through this analysis. Two individuals shown in figure 18, 3971-4 and -23, tend to develop their tallest stems at Stanford; 3971-18 becomes definitely tallest at Timberline; and 3971-17 is tallest at Mather, comparing favorably with the Yosemite Creek form. Many individuals are similar to those found in the Timberline population, and others, such as 3971-12 and -19, even match in size, earliness, and frost resistance the high-alpine forms from Big Horn Lake, 850 m. higher than Tenaya Lake.

In viewing the evolutionary possibilities in a population such as that from Tenaya Lake, one is impressed by the kind of variation it contains. Most of the forms that could have been fitted for lower altitudes seem to have been eliminated by constant selection, for they are infrequent, but those that might have tolerated the more severe conditions of a considerably higher elevation exist apparently without difficulty.

THE TUOLUMNE MEADOWS AND TIMBERLINE POPULATIONS

The Tuolumne Meadows population came from 2620 m. elevation on the west side of the Sierran crest, the Timberline population from 3050 m. on the east side. Both are referable to *lanulosa alpicola,* along with the
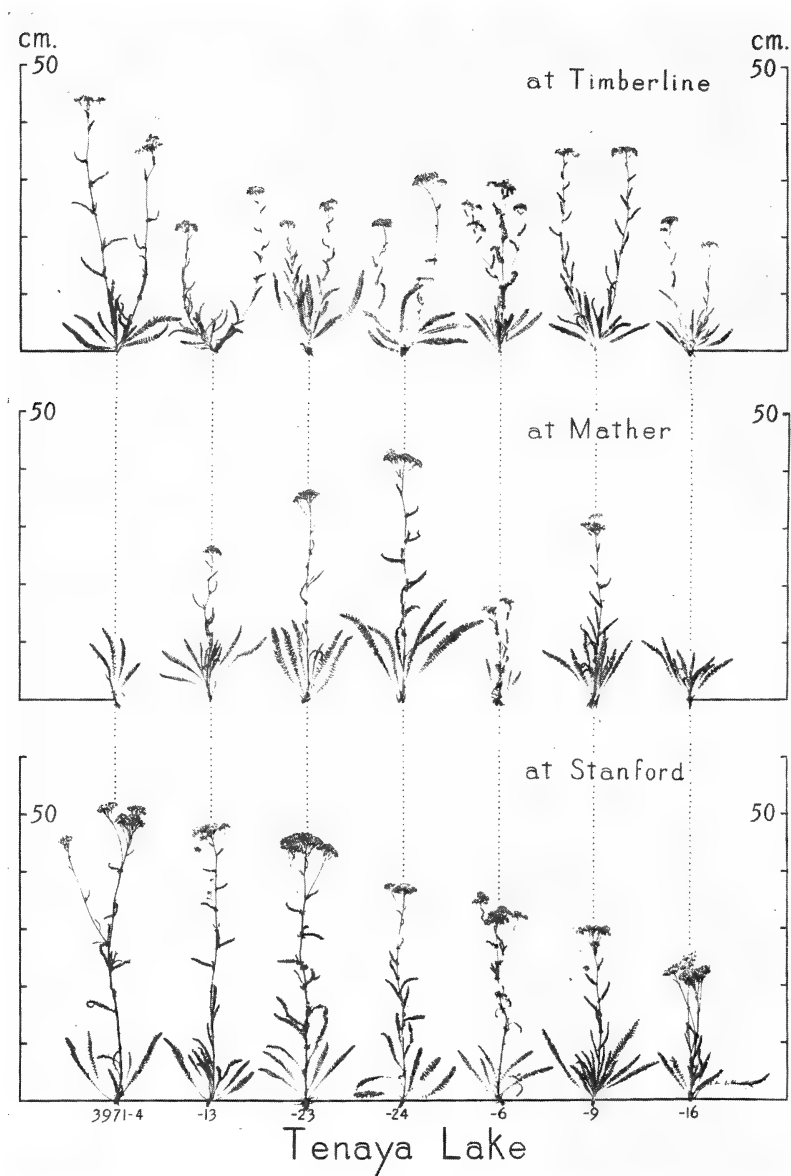
FIG. 18. Responses of clones of 7 plants of the Tenaya Lake population from the high Sierra Nevada (2500 m.) at Stanford, Mather, and Timberline. The numbers at the bottom are those of the individual plants; their records may be traced further in table 13.

other populations from Tenaya Lake up to Big Horn Lake, and both inhabit sunny slopes or meadows. These populations do not differ significantly in their reactions at the transplant stations, as may be seen by comparing them in table 19 (p. 63).

Weather records from high altitudes in the Sierras are scarce. Those from Ellery Lake, at 2890 m., are taken from an elevation intermediate between those of the habitats of the two populations considered here, and, as previously explained, represent a climate somewhat milder than that of the Timberline garden. In table 21 (p. 69) the data for Ellery Lake may be compared with those for Huntington Lake for an impression of the climatic differences that characterize the native habitats of these subalpine forms of *Achillea* and those of the fir belt at Aspen Valley and Yosemite Creek. Since both races lie dormant under a winter snow pack, summer temperatures are the most critical to them. At Ellery Lake the July mean maximum and minimum temperatures are 3.39° and 3.50° C. lower than at Huntington Lake, and the growing season is 47 days shorter, as shown in figures 4 and 5 (pp. 14, 15).

The populations from Tuolumne Meadows and Timberline are markedly shorter at Stanford and Mather than are those from Aspen Valley and Yosemite Creek, and are considerably earlier in flowering at all three stations. The Tenaya Lake population is transitional between these but tends to be more subalpine. From this comparison it is clear that a relatively small change in climate is associated with a significant change in the composition of native populations of *Achillea,* a change that determines the success or failure of these plants at high altitudes.

A study of the records of individual plants in tables 14 and 15 (pp. 59, 60) will reveal some of the ecological possibilities within the Tuolumne Meadows and Timberline populations. Each contains some plants that react like those from lower altitudes, and others that are more like those from an elevation still higher than Timberline. The plants 3972-13 and -20 from Tuolumne Meadows are tall at Stanford and Mather, like plants from a little farther down the mountains, but they are subalpine in their early flowering. The Timberline plant 3780-20 is a counterpart of the more alpine-like variants from Yosemite Creek, such as 3970-10 and -20, both in size and in lateness of flowering, but it is highly frost-resistant and is able, even though late, to set seed in its native habitat. The tall, robust Timberline individual 3780-1 is indistinguishable from average plants of the Tenaya Lake population in all the three environments. A plant of especial vigor in all environments is 3972-24 from Tuolumne Meadows.

A particularly interesting group with respect to selection for higher altitudes consists of the short, dwarf, early-flowering variants that are like plants from the Big Horn Lake population. Examples include 3972-9 from Tuolumne Meadows and 3780-7, -8, and -25 from Timberline. The importance of this kind of variability is obviously not evident from mean statistical values of populations.

The percentage of plants resistant to heavy frosts increases with altitude, for two weeks of frost at Timberline in September 1946 injured the inflorescences of 6 of the 29 plants from Tenaya Lake, and 2 of the 28 from Tuolumne Meadows, but none of the 27 plants from Timberline.

THE BIG HORN LAKE POPULATION

This extreme alpine comes from the upper altitudinal limits of *Achillea* on the Sierran transect. In the habitat of this race at 3350 m. the growing season is usually so short that even this rapidly developing form cannot ripen its fruit, but in the Timberline garden, 300 m. lower, it matures without fail. There it excels the Timberline native in number of stems produced and in the rapidity of their development after the snows melt from the garden. The stems elongate immediately, even before a leafy rosette has developed to nourish them. At Timberline it attains its best development, as is obvious from figure 19, which shows a sample of 7 individuals that cover much of the range of variation in the population. It is the only form with stems consistently tallest at Timberline, as can be seen from table 19 (p. 63). The illustration does not fully present the situation at Mather, for, though this alpine grows very poorly, 8 out of 12 plants flowered there in one year or another.

The small sample of 12 transplants from Big Horn Lake represents fairly adequately this restricted population from high altitude. From table 19 it can be seen that this truly alpine population flowers two weeks earlier at Stanford than any of the subalpine populations from Tenaya Lake to Timberline, and it is also four days earlier at Timberline. The differential in earliness is even more noticeable at the time the seeds mature at Timberline, and is probably very important for the survival of this population at Big Horn Lake. None of the inflorescences were injured by the two weeks of heavy frost in September 1946, though some rosette leaves were injured.

A detailed report of the performance of the individuals of this form is presented in table 16 (p. 61). Although there is appreciable individual variation, this population appears to be more uniform in its reactions than any of the three preceding subalpines. The plants from Big Horn Lake

react uniformly like the few short, early-flowering and early-maturing plants found in the populations from Timberline, Tuolumne Meadows, and Tenaya Lake. Apparently a fairly homogeneous alpine population like that from Big Horn Lake could be selected from these subalpine populations.

Achillea from high altitudes in the Sierra Nevada consists of variable populations containing both earlier- and later-flowering fractions that would enable any one of them to populate neighboring areas if the need
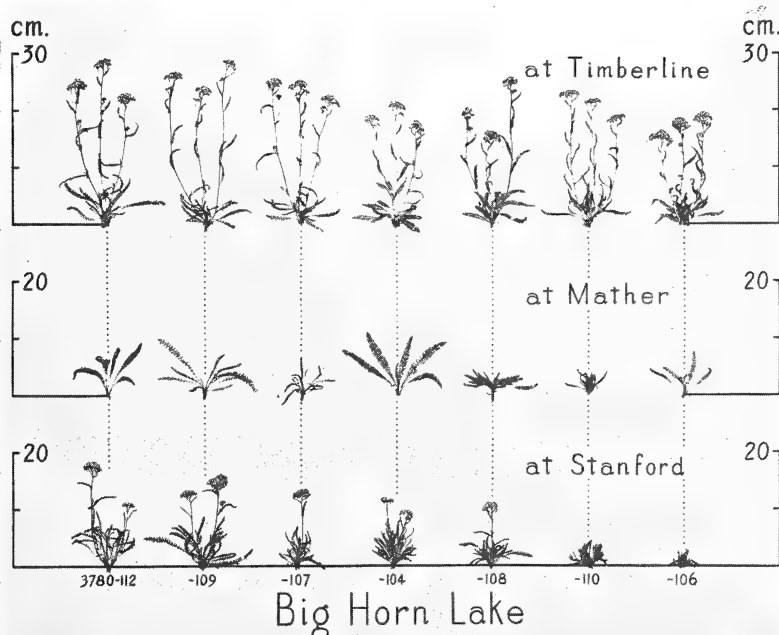
FIG. 19. Responses of clones of 7 plants of the Big Horn Lake population from the crest of the Sierra Nevada (3350 m.) at Stanford, Mather, and Timberline. The numbers at the bottom are those of the individual plants; their records may be traced further in table 16.

arose. Cross-pollination and wind transport of the light seeds aid in blending and shuffling the populations. Selection is nevertheless strict enough even under these conditions to produce a gradual trend that is noticeable from the increase in the percentage of short, early-flowering, and more frost-resistant individuals at increasingly higher altitudes.

The Big Horn Lake population is probably distinct enough from the others to be classed as a separate alpine ecotype. It can be separated statistically from a subalpine ecotype that would include the Timberline, Tuolumne Meadows, and Tenaya Lake populations. These are scarcely

distinguishable from one another, even by the present rather elaborate methods of uncovering differences. It must be recognized, nevertheless, that the taller population from Tenaya Lake is probably better able to utilize the slightly more favorable climate of its native environment than, for instance, the form from Timberline, and that the latter, in turn, is moderately superior in its own environment.

ACHILLEA MILLEFOLIUM FROM NORTHERN EUROPE

Two populations of *Achillea millefolium* were investigated at the three stations, one from the coast of Denmark, and the other from 13° farther north in Swedish Lapland, at 420 m. altitude. The climates from which these came are very different. The Danish locality has a January mean temperature of 0° C. and a July mean of 16°, whereas the Lapland station (Abisko) has corresponding temperatures of −15° and 11.7°. In both climates the summers are sufficiently humid to encourage growth.

The range of mean temperatures at the Danish locality corresponds to those of a California station between Lake Eleanor and Huntington Lake (table 21, p. 69), but the climate is, of course, much less continental. Snow seldom lies on the ground for extended periods. The winter in Lapland is colder than at any place along the Sierran transect, but the July mean temperature corresponds to that at Ellery Lake. Snow is on the ground for an average of 203 days per year, which roughly corresponds to the situation at Timberline Station, but at Abisko snow melts a month and a half earlier in the spring. The summer climates at the northern latitudes are further mitigated by the long days. At Abisko, there is continuous daylight between June 9 and July 5.

THE DANISH COASTAL POPULATION. Seedlings from a single plant of a low, depressed coastal form from the sandy west coast of Sjaelland, near Skelskör, were grown in the three environments of the transplant stations. They grew considerably taller at both Stanford and Mather than in their Danish habitat, probably because of higher temperatures during the growing season, as will be seen in chapter IV; and they flowered a month earlier at Stanford than they would have in their native environment. This population was variable, as is shown in table 17 (p. 61), in spite of its origin from a single plant.

This form from a mild winter climate without much snow remained green and active the entire year at Stanford, though less winter-active than the forms from the California coast. It was as vigorous at Mather as at Stanford, but proved to be more palatable than the American species to

rodents, by whose foraging the plants were so weakened that most of them died.

At Timberline they developed most peculiarly, producing tiny, matted rosettes of minute leaves that by the end of the season were scarcely more than 1 or 2 cm. high. No flowering stems were produced. After the fourth winter, 6 of the original 11 plants were still alive. The persistent rhizomes grew a few centimeters each year, although it is difficult to see how sufficient food was synthesized by the minute leaves to support even this much growth. None of the races from California react in a comparable way, but a taller inland form from woodlands northwest of Copenhagen behaves similarly, as already described by the writers (1940, p. 307).

THE LAPLAND POPULATION. Twenty seedlings of a population from Abisko, Swedish Lapland, were included in the transplant experiments. It was especially interesting to determine whether these Achilleas from 2° north of the Arctic Circle were better able to develop at Timberline than the Danish forms.

Swedish Lapland at the altitude and latitude of Abisko has a fairly continental climate with winters shorter than at Timberline. The snow melts around May 10 as compared with July 1 at the alpine station in California. Although the mean temperatures during the summer at Abisko are within 1° of those at Timberline, the summer climates are widely different. Abisko has continuous daylight, consequently much milder nights, whereas there are wide diurnal fluctuations in temperature at Timberline, where frosts are to be expected at any time during the summer growing season. The summer climate of Abisko is therefore more equable and generally favorable for plant growth than is that of the high Sierra Nevada.

The *Achillea* population from Abisko, unlike the Danish coastal form, becomes winter-dormant at Stanford, as might be expected of plants native to a climate with severe winters. Once spring growth starts, however, it develops more rapidly than the Danish forms and flowers approximately two weeks earlier both at Stanford and at Mather (table 19, p. 63). The shorter days in California do not impede the flowering of these arctic plants, for they flower freely at Stanford in late April at a time when they would still be covered by snow in Lapland (table 18, p. 62). Their stems are slightly shorter both at Stanford and at Mather than in their native environment. Like the Danish coastal form, the Lapland race at Mather was heavily grazed by rodents that killed most of the transplants.

At Timberline the Lapland individuals reacted in the same manner as that described above for the Danish form, persisting as tiny, slowly spreading mats of leaves less than 2 cm. above the ground. Out of 20 transplants originally set at Timberline, 14 were still alive after the fourth winter, some having developed mats up to 30 cm. across. Only 2 individuals during this time attempted to produce flowering stems, and these stems were immature and inconspicuous at the end of the growing season.

From their reactions at the transplant stations it is clear that physiologically the Lapland form is closely allied to the Danish. The two belong to distinct climatic races or ecotypes, however, for the subarctic Lapland form differs from the Danish in being winter-dormant, and in reaching the flowering stage more rapidly.

There are basic physiological differences between the California alpines and the subarctic form from Lapland. This is strikingly evident in the garden at Timberline, where the California forms develop vigorously with abundant flowering, and the Lapland form remains a low, barely surviving vegetative mat. At Timberline the nonflowering *A. millefolium* from northern latitudes in Europe contrasts also with the freely flowering *borealis* from Seward, Alaska, as already described by the writers (1940). After interpreting these observations, one should expect northern races of *millefolium* to require a higher minimum temperature for flowering than either the alpine forms of *lanulosa* or the arctic forms of *borealis*. This conclusion was further substantiated by the experiments under controlled conditions which are described in the following chapter.

IV

GROWTH RESPONSES UNDER CONTROLLED CONDITIONS

The strikingly different responses at the three transplant stations of the various climatic races of *Achillea* described in chapter III lead naturally to inquiries regarding the physiological characteristics that determine these responses. A logical experimental approach to such inquiries is to carry the transplant method a step farther by studying the growth of clones of representative plants under different controlled conditions, changing only one variable at a time. From such observations conclusions may be reached that can be used in charting the course of future studies on the comparative physiology of climatic races, now an undeveloped field. As a step in the search for clues to the mechanism of natural selection, the study of the growth of plants under controlled conditions can be planned with the conditions of their natural habitats in mind.

Through the kind invitation of Dr. F. W. Went, one of the writers, Hiesey, was privileged to utilize greenhouse facilities of the California Institute of Technology at Pasadena for preliminary studies on the growth of *Achillea* under controlled conditions. This chapter is based on such experiments conducted between January and May 1944. One of the immediate objectives of this work was to determine the effect of differences in temperature and in length of day upon races from very different altitudes and latitudes.

METHODS

Selected individuals of the more important climatic races discussed in the preceding chapters were used in these studies. These were propagated vegetatively in November 1943, when the plants were dormant or relatively inactive in the garden at Stanford. As many as a dozen equal divisions were taken from each individual and kept in a greenhouse to strengthen. During December, growth of the lowland and mid-Sierran races was rapid, but in the subalpine and alpine forms it was largely restricted to roots and rhizomes.

Early in January the plants were taken to Pasadena and repotted in coarse river sand in 6-inch pots. The sand assured good drainage and aeration of the roots, and a ball of soil from the first potting was retained around the roots. For one week prior to the experiments, the plants were kept in a uniformly lighted greenhouse for conditioning. During the entire period they were watered at least twice daily, once with Hoagland's solution to ensure an ample supply of mineral nutrients.

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The air-conditioned greenhouses at the California Institute of Technology, where the experiments were conducted, have been described by Went (1943). They consist of two units in which temperature and humidity can be independently controlled. Each unit has two parts, one of which receives natural illumination through a glass roof; the other, used for artificial illumination, is a closed room equipped with batteries of fluorescent lamps controlled by a time clock. In addition, cold chambers large enough to accommodate a considerable number of plants have been built next to the greenhouses. By placing the plants on trucks that can be wheeled from one compartment to another, it is possible to subject them to a variety of experimental conditions, as, for example, different temperatures during the day and night. In practice, most transfers involving different temperatures were made at 8:00 A.M. and 4:00 P.M., thus dividing the day into an 8-hour and a 16-hour period.

A continuous stream of air maintained at a constant relative humidity (approximately 70 per cent in the *Achillea* experiments) passes through the compartments at all times; its flow is dispersed by baffle plates and electric fans. In the compartments illuminated by natural daylight, a film of water is passed over the glass roof during the warm hours of the day to help maintain constant temperatures. During this period the intensity of the sunlight reaching the plants is about half that outside. Fluctuations of light intensity due to cloudiness and the diurnal shift in the sun's position influence growth of plants, but the two naturally illuminated compartments are alike in this respect and receive equal amounts of light.

Figure 20 summarizes the physiological experiments at Pasadena. It shows the experimental conditions tried, the plants used for each condition, and something of their growth. Two series of comparisons were made: (1) between propagules of one individual under different conditions, and (2) between individuals of different races under uniform conditions. In interpreting the results, the reactions of all propagules of one individual were compared with those of another individual. The experimental pattern shown in figure 20 made it possible to check the consistency of an individual's growth reactions under a series of experimental conditions.

The experiments were started January 17. At this time all the plants had begun to grow at least to some extent. The lowland forms were especially active, because at this time they normally begin their period of most rapid growth. The subalpine and alpine races, normally dormant

Fig. 20. Summary of the physiological experiments in the air-conditioned greenhouses in Pasadena, showing the various experimental conditions, the individuals of *Achillea* used, and the degree of vigor and flowering of the clones. See text.

in January, were slightly active under the stimulus of greenhouse conditions. The plants as a whole were in excellent condition for rapid growth during the experimental period.

Beginning January 17 and ending May 10, when most of the experimental work was concluded, weekly notes and measurements of growth were recorded on printed forms. The records included height and width of plants, lengths of longest stems and rosette leaves, number of stems, approximate number of rosette leaves, date of first flowering, general vigor, and presence of disease or insects. The weekly notes were supplemented at about the beginning and again toward the end of the experiments by a photographic record made with a 35-mm. camera. This record was very useful, and the help of Dr. Harlan Lewis in taking the pictures is gratefully acknowledged. At the conclusion of the experiments, herbarium specimens were made of the experimental plants.

RESPONSES OF THE RACES

Marked differences were observed in growth responses of the altitudinal and latitudinal forms to different sets of temperatures. Responses to light were also observed. No definite photoperiodic effects were found in races from different latitudes, but races from high altitudes in the Sierra Nevada required more light for flowering than did lowland races from the same latitude. These physiological differences between the races can be related to the climatic differences between their environments.

THE SAN GREGORIO AND SELMA FORMS. Two individuals that represented the coastal and the San Joaquin Valley races in these experiments are shown in figure 21 as they grew in the garden at Stanford. Both these races thrive at Stanford, as is shown in chapter II, although the climates of their original habitats differ widely in temperature, as is illustrated by the curves (figs. 2 and 3) for Point Reyes and Fresno, respectively.

In the controlled greenhouses the propagules of these two plants showed significantly different responses to temperature treatments. The San Gregorio form grew vigorously when kept at 17° C. during the day and 7° C. at night, temperatures at which the Selma form was able to grow only very slowly. Conversely, the Selma plant throve at the high temperature of 26° C. sustained day and night, a condition that was detrimental to the best growth of the San Gregorio form. At the intermediate temperatures of 17° during the day and 13° at night, the two forms were equally active and vigorous, as can be seen from the summary in figure 20.

The rate of growth of these two plants under 8 hours of daylight at 17° C. and two different night temperatures is shown in figure 22 by curves showing heights of longest stems measured at periodic intervals. Under a cold night of 7° C. the San Gregorio form grew vigorously and flowered, whereas the Selma plant grew but little and produced no flowers. With the warmer nights of 17° C. the Selma form grew more

FIG. 21. A plant of the coastal San Gregorio population (left), and another from the San Joaquin Valley at Selma (right), growing in the garden at Stanford. These individuals were used for study under controlled conditions. The black-and-white scale is 10 cm. high.

rapidly and much better; it produced buds but did not reach flowering. On the other hand, the San Gregorio form grew more slowly with the warm nights and reached no more than half the height of the Selma plant, although it flowered.

Figure 23 shows the growth curves of divisions of the same two plants under natural day length. At a constant day and night temperature of 26° C. the Selma form grew vigorously and flowered, but the San Gregorio form was weak, though it also flowered. With a day temperature of

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17° C. and a night of 13° both forms grew vigorously and flowered freely, becoming even taller than in the garden at Stanford, and thus demonstrating that under these conditions their temperature tolerances overlap.

Other experiments with the same two plants yielded results that were consistent with these. For example, with 8 hours of daylight at 26° C. and 16 hours of darkness at 17°, the Selma plant flowered and grew definitely more vigorously than the nonflowering one from San Gregorio,
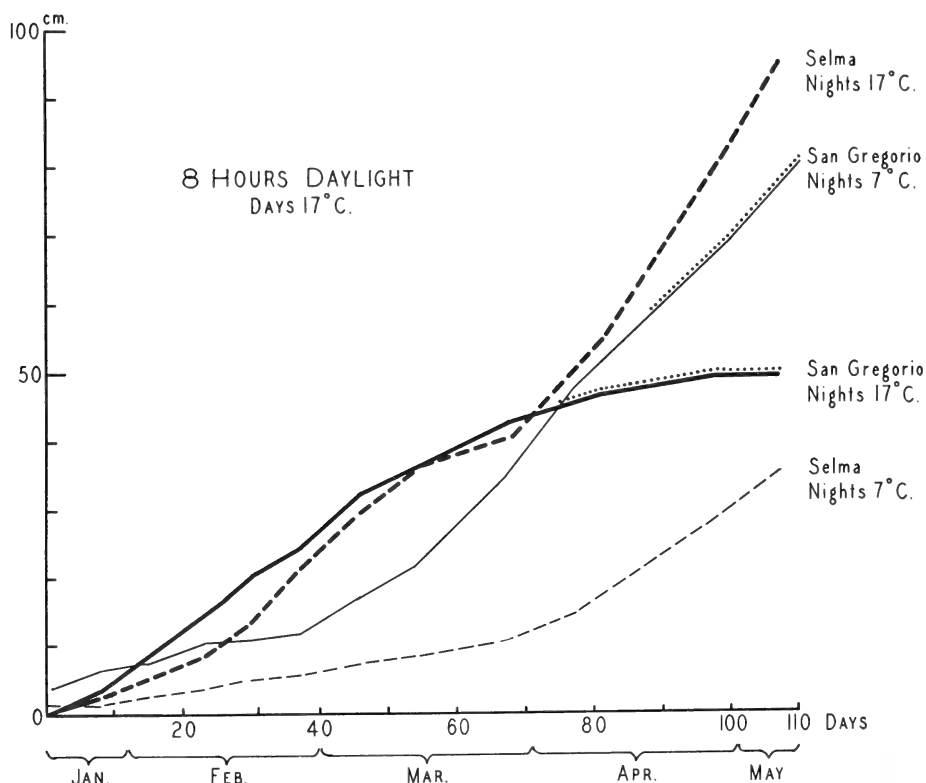
FIG. 22. Growth curves of stems of clones of the coastal San Gregorio (3777-7) and the interior Selma (4074-101) plants under cold and cool night temperatures. Measurements were made at weekly intervals. The dots above the curves indicate open flowers. See text.

but when the nights were kept cold at 7°, the day temperatures remaining at 26°, the San Gregorio plant grew at least as rapidly as the Selma, both developing to the bud stage (fig. 20).

A marked increase in vigor and speed of development was apparent in both these forms when supplementary light from fluorescent lamps of approximately 650 candle-power intensity was supplied. With 8 hours of daylight at 26° C. plus 16 hours of artificial light at 17°, both plants
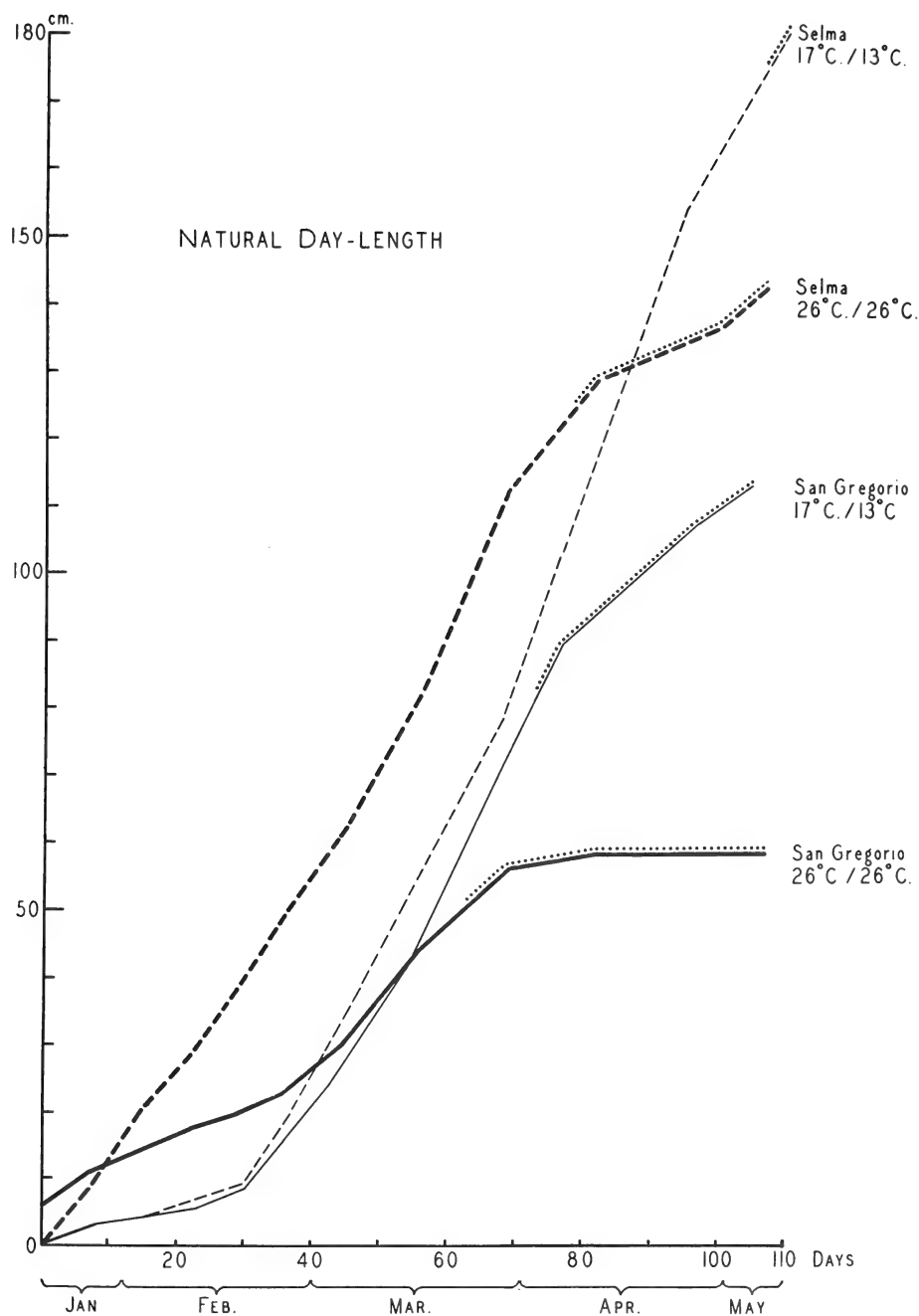
FIG. 23. Growth curves of stems of clones of the coastal San Gregorio (3777-7) and the interior Selma (4074-101) plants under warm and cool temperatures. The temperatures shown are those of day and night, respectively. Measurements were made at weekly intervals. The dots above the curves indicate open flowers. See text.

flourished and flowered early. Without the supplementary light, but at the same temperatures, both were much weaker, especially the San Gregorio, which did not even flower. Evidently the short 8-hour day at these relatively high temperatures is more limiting to the San Gregorio plant than to the one from the hot Selma climate.

Given proper conditions of temperature, both forms are able to produce flowers when the days are of varying length, including an 8-hour day, one of natural length, and one of 24 hours. They are therefore not specialized in their photoperiodic requirements.

Along the coast of central California the temperatures range from 17° to 22° C. during the day and from 5° to 10° C. at night during the winter, when native Achilleas are in their most active period of growth (cf. fig. 2, p. 11). This temperature range is comparable with the controlled condition of a 17° day and a 7° night, an environment that proved favorable for vigorous growth of the San Gregorio form, but unfavorable for that of the Selma. At Stanford the Selma form begins its most active growth later than the one from San Gregorio. Such differences in seasonal periodicity in climatic races are probably to a large extent governed by temperature. From the results observed under controlled conditions, the San Gregorio form would be expected to grow poorly in the San Joaquin Valley except during the early spring, when temperatures are relatively low.

The ranges of temperature tolerated by the San Gregorio and Selma races are clearly different, the former thriving better at cooler ranges, the latter at warmer. At intermediate temperatures there is an overlapping tolerance. The differences in vigor probably reflect differences in the rates of assimilation and respiration of the two forms at various temperatures. The problem of the physiological mechanisms involved is an extension of the present problem that would require a different method of investigation.

REACTIONS OF OTHER LOWLAND FORMS. A plant of the maritime Bodega form described in chapters II and III reacted to conditions in the controlled greenhouses in much the same way as the San Gregorio form. Both thrived at the intermediate cool temperatures, 17° C. and 13°, and grew very poorly at the sustained high temperature of 26° (fig. 20). At the lower temperatures the leaves were smaller and thicker, and the stems sturdier, like those of plants grown outdoors. The Bodega form differed from the San Gregorio chiefly in its slower rate of stem elongation, shorter

internodes and stems, and later flowering. The growth curves shown in figure 24 illustrate these differences.

Data from a typical plant (3965-4) of the Clayton form of the foothill race show some interesting responses: poor growth with weak, precocious flowering stems under a constant day and night temperature of 26° C.,
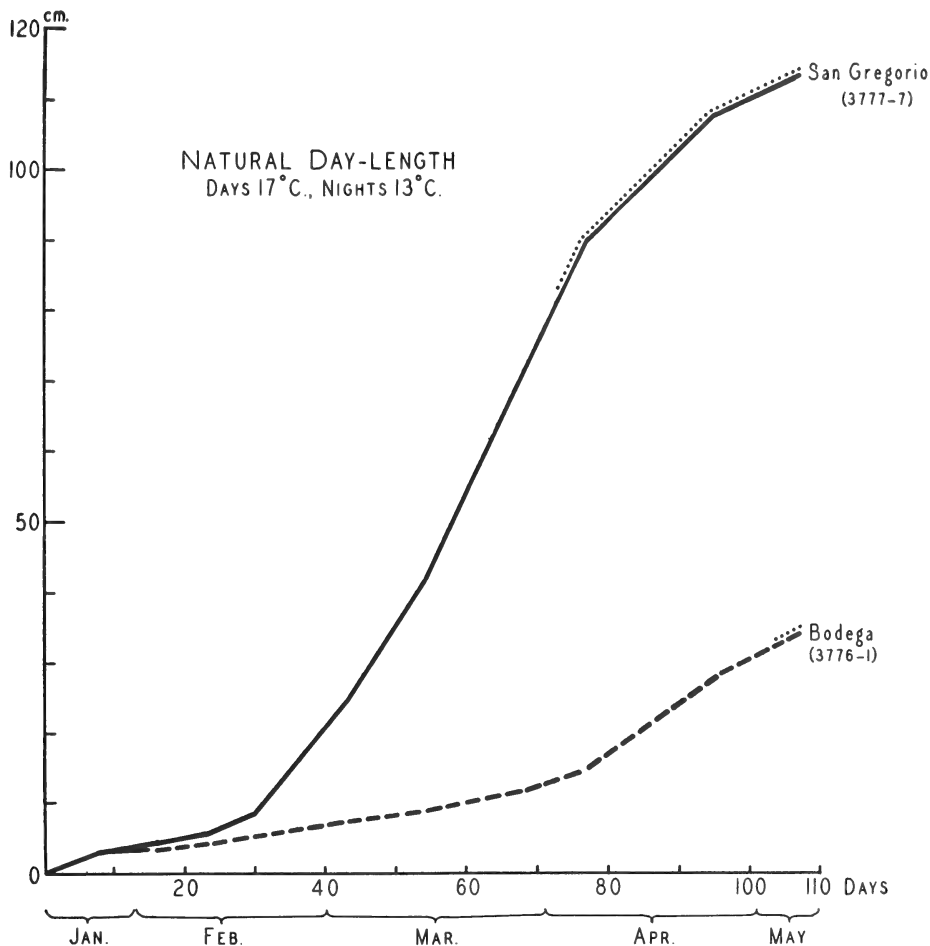
FIG. 24. Growth curves of stems of a dwarf maritime form (Bodega) and a tall coastal form (San Gregorio) under identical conditions. Measurements were made at weekly intervals. The dots above the curves indicate open flowers.

but vigorous growth and excellent flowering with a day temperature of 17° C. and a night of 13°. At both sets of temperatures the clone grew under a natural length of day.

It will be recalled from chapter II that the foothill forms grow vigorously during the cool winter months and become dormant in early

summer. In the cool greenhouse compartment with a 17° C. day and a 13° night, the Clayton plant remained green until observations were ended in July, producing new stems long after the divisions growing both at 26° C. and outdoors at Pasadena were dormant. This suggests that temperature may be a critical factor initiating summer dormancy in the foothill race. In the garden at Stanford plants of this race invariably become dormant as temperatures rise in late June, even though an adequate supply of moisture is provided.

THE SIERRAN RACES. The Mather form was represented in the experiments by a slope plant, 1315-1, whose reactions at the transplant stations have been studied extensively (see the authors, 1940, p. 319). It is among the vigorous, winter-active plants at Stanford, a fact which indicates a degree of fitness for the Coast Range environment, but it has also survived for more than ten years at Timberline, where during four seasons it has flowered early enough to mature some seed. It is unique that a plant most vigorous at Stanford should survive so well at Timberline.

In the controlled greenhouses also it succeeds under an unusually wide range of conditions, as can be seen from figure 20. At the constant high temperature of 26° C. its vigorous growth and flowering were comparable with those of the Selma plant, whereas at lower temperatures, with days of 17° C. and nights of 7°, it was not far behind the cold-loving San Gregorio form, although it did not flower. With days at 17° and nights at 13°, this plant, like those from the Coast Ranges and the San Joaquin Valley, flowered and developed vigorously. It attained its most outstanding vigor, however, and far outperformed both the Selma and the San Gregorio plants, with warm days at 26° C. and cool nights at 7°. During June, when the native Achilleas at Mather make their most rapid growth, hot days and cool nights prevail (see temperature curves for Lake Eleanor, fig. 4, p. 14).

The winter-dormant Aspen Valley plant, 3969-16, was much less adaptable, and although morphologically similar to the Mather plant, it behaved very differently under almost all the controlled conditions. It grew rapidly with a high day temperature of 26° C. and a cold night of 7°, being vigorous and flowering much as did the Mather plant, but with the higher night temperature of 17° it declined rapidly a month after the beginning of the experiment. With a cool day temperature of 17° C. and a night of 13° this form grew very slowly and remained vegetative, in marked contrast with the vigorously active forms from Mather and lower elevations.

The subalpine plants from Tenaya Lake and Timberline remained dormant in the coldest conditions and developed rosettes at higher temperatures. Neither flowered under any of the controlled conditions, except when additional illumination was supplied. When fluorescent light of approximately 650 candle power was provided at 17° C. for 16 hours following 8 hours' exposure to natural daylight at 26°, all the plants from the higher altitudes developed rapidly and flowered. Under these conditions the Aspen Valley plant flowered one month after the experiment was started, and similar responses were observed in the Tenaya Lake and Timberline forms. That this stimulation is not a specific photoperiodic effect is suggested by the fact that the Aspen Valley plant flowered under an 8-hour day.

In figure 25 the responses of a Timberline plant to various temperature and light treatments are compared with those of the San Gregorio form from the coast. Specimens of both grown in the garden at Stanford are also shown. Under an 8-hour day at 17° C. and a night at 7°, the alpine plant did not grow, but remained as a semidormant rosette until midsummer and then died. Under the same conditions the San Gregorio plant grew vigorously and flowered freely. Increasing the day and night temperatures had little effect on the alpine except to stimulate temporary vegetative growth, but later these gains were followed by a decline in vigor, when probably the stored food in the rhizomes had been consumed. The leaves shown in figure 25 were taken at the time of maximum growth. The propagules grown under a 26° day and a 7° night became very weak by July, while another, under conditions the same except that the night temperature was raised to 17°, declined even faster. The higher temperatures also reduced the growth of the coastal form, as is shown in the figure. This observation suggests the deleterious effect of increased respiration at higher temperatures under a limited supply of light. Supplementary illumination greatly stimulated growth, but the response was greater in the alpine form than in the coastal. These growth responses show that the two forms have very different physiological balances, and these balances are differentially influenced by external conditions.

In evaluating the experimental results with the races from higher altitudes, it should be remembered that the light intensity in the controlled greenhouses was reduced to approximately one-half that found outdoors, and that the intensity of the fluorescent light was much less. The intensities prevailing at higher altitudes during midsummer are therefore far greater than any attained in the air-conditioned greenhouses. The large, thin leaves produced by the subalpine and alpine plants under the con-

trolled conditions were of a type produced in shade, and indicate that the light intensity was not sufficient for normal development. Lowland and mid-altitude forms, on the other hand, attained a more normal character of growth, indicating that the light for these was probably adequate.
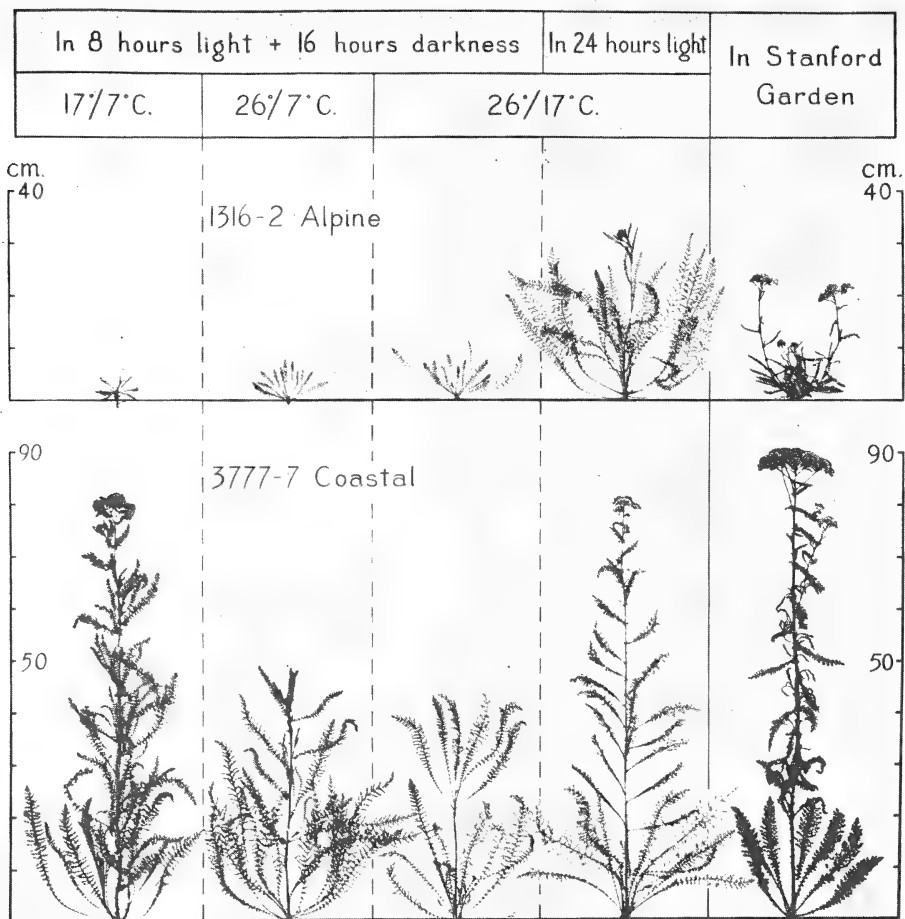
Fig. 25. Growth responses under controlled conditions of a clone of an alpine *Achillea lanulosa* from 3260 m. elevation compared with those of a clone of *Achillea borealis* from the coast.

Herbarium specimens from the same clones in the garden at Stanford are shown at the right. The temperatures indicated are for day and night, respectively. See text.

These facts point to the conclusion that alpine and lowland races differ in the light intensities required for their maximum growth.

THE LEEVINING FORM. It will be recalled from chapter II that in the garden at Stanford the Great Basin races differ in appearance and perio-

dicity from those from the high Sierras. One plant, 2460-2, from near Leevining, California, was grown in the controlled greenhouses, and its responses emphasize these differences. The reactions of this plant at the mountain stations have already been reported (1940).

In the controlled experiments this Leevining plant grew best and flowered rapidly under an 8-hour day at 26° C. and a night at 17°, a combination under which the plants from the high Sierras were very weak and those from lower altitudes grew relatively but little. The greatest efficiency of the Leevining form is evidently attained under conditions quite different from those required for the races previously discussed. With a 26° day and a 7° night, no progress in development was made during seven months, the plant remaining as a healthy rosette of unchanged dimensions. Under these conditions the Mather and Aspen Valley forms developed most vigorously and flowered freely.

FORMS FROM NORTHERN LATITUDES. Plants from Seward, Alaska, at 60° north latitude, from Denmark at 55° north, and from Abisko, Swedish Lapland, at 68° north, all grew well under the wide range of conditions tried in the controlled greenhouses, but they reacted very differently from the plants originating in California.

The plant from Seward, 2443-3, of *Achillea borealis typica,* was previously studied at the transplant stations (1940, p. 319, table 26). It grew very poorly at Stanford and Timberline, but with normal vigor at Mather, where it was very floriferous. In the greenhouse experiments it grew well under all the conditions indicated in figure 20, but it was the only plant of the experimental series that did not flower at all. The growth of the rosette varied with the temperatures and the period of illumination, higher temperatures and longer days being directly correlated with greater growth. Leaf samples from the rosettes of this plant growing under a series of contrasting conditions are shown in figure 26. Their generally healthy growth in all the environments tried indicates a capacity of the plant to grow under a wide range of conditions. Apparently the balance between the rates of photosynthesis and of respiration ensures a safe margin of net assimilation over a wide range of temperatures. This may be of survival value to this plant from a climate with great seasonal changes.

Somewhat similar responses were observed in two plants of *Achillea millefolium* from Abisko, Lapland. Both of these remained vegetative under most of the conditions and responded to higher temperatures and increased light with increased growth. The leaves, which are inherently

8

smaller than those of the Seward plant, were not modified so much, but the trend was in the same direction. It will be recalled from chapter III that at Timberline the Lapland form grew poorly but with great tenacity, developing minute rosette leaves year after year. The leaves produced at the cool day temperature of 17° C. with cold nights at 7° were rather comparable to those produced at Timberline.

Both the Lapland plants were able to flower under an 8-hour day at 26° C. and a 16-hour night at 17°, a condition under which the Great Basin form from Leevining also flowered. The Lapland form, however, when supplied with 16 hours of supplemental fluorescent light at these
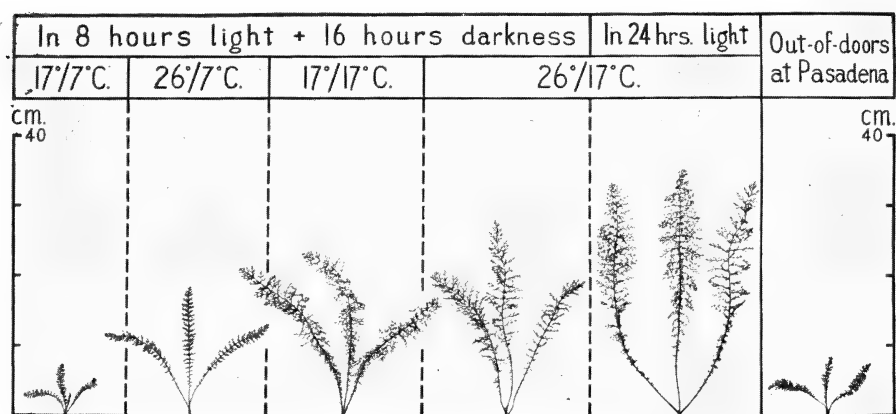
Fig. 26. Growth responses, under controlled conditions and out of doors, of a clone of a plant (2443-3) from Seward, Alaska. Specimens taken at the end of the 3½ months' experimental period. The temperatures indicated are for day and night, respectively. See text.

same temperatures did not flower, but responded with increased rosette growth like the Seward plant.

A form of *Achillea millefolium* from the woodlands of Denmark responded unexpectedly to the varied environments of the controlled experiments. It flowered under an 8-hour day, under natural day length, and under continuous illumination, but only when exposed to warm days of 26° C. combined with cool to mild nights of 13° or 17° (see plant 1808-1, fig. 20). It grew especially rapidly under 8 hours of daylight at 26° C. and 16 hours of supplemental light at 17°, flowering one month after the experiment was started. Without the supplemental light, flowering was delayed one month. At lower temperatures, as under natural day length at 17° C. with nights at 13°, growth was slow but healthy,

and no flowering occurred although the experiment continued until July 19.

These observations are in harmony with those made on this plant at the transplant stations. At Stanford it grows slowly during the winter and does not flower until late in the season after temperatures have risen. At Timberline it remains perennially a tiny vegetative mat, but there in a warmer slope garden in more favorable seasons some immature stems develop (see the authors, 1940, fig. 121). All the evidence points to the conclusion that flowering in this Danish form is dependent upon relatively high temperatures. In July in Denmark the days are long and the temperatures approximate those of the controlled greenhouses in which this plant flowered.

Another plant, 2442-1, representing a dwarf maritime ecotype from the Danish coast, was grown in only two of the controlled greenhouse environments and therefore is not included in the summary diagram, figure 20. When this maritime form was grown under a full natural day with cool temperatures of 17° C. during the day and 13° during the night, it flowered, producing 9 dwarfed stems up to 17 cm. long resembling those developed on the cool Danish coast (chapter II, p. 40). When grown under an 8-hour day at 26° C. and a mild night at 17°, it flowered a month earlier than in the first condition, producing stems up to 47 cm. long, comparable in height with those grown in the warmer gardens at Stanford and Mather (see table 17, p. 61).

These experiments are helpful in interpreting the physiological capacities of *Achillea millefolium* from northern latitudes. This species apparently prospers at relatively high temperatures, developing with great rapidity under such conditions, especially when given additional light. Its forms flower in their native northern environments during the brief but warm summer, with long days and mild nights. The winter-active coastal forms of *A. borealis* from central California, on the other hand, thrive and flower at lower temperatures despite their more southern origin.

DISCUSSION

In studying the reactions of the various races under controlled conditions as summarized in figure 20, one notices that all the California members of *Achillea borealis* from the coast and across the San Joaquin Valley, and *A. lanulosa* from Mather, thrive and flower freely under a cool day temperature of 17° C. and a mild night of 13°, whereas *A. lanulosa* from higher altitudes and the Great Basin, and *A. millefolium* from northern Europe, remain vegetative and grow slowly. Under warm days at 26° C.,

with nights at 17°, only *lanulosa* from the Great Basin and *millefolium* from northern Europe flourish. There is a difference within *borealis* between the coastal form, which thrives best under the cool day of 17° C. and cold nights of 7°, and the Selma form, which grows more successfully at higher temperatures. Within *lanulosa* there are at least three groups: the mid-altitude Mather and Aspen Valley forms, which flourish under a warm day temperature of 26° C. and a cold night of 7°; the high-altitude forms, which seemingly require more light than was furnished under the experimental conditions at Pasadena; and the Great Basin form from Leevining, with a reaction parallel to that of *millefolium*.

By exploring the behavior of races from different environments under sets of known conditions so devised as to make physiological interpretations possible, we can begin to understand how such races are equipped to meet the requirements of their natural environments. The present study is a beginning in this direction, and suggests methods for further investigation. Through similar approaches it should be possible to develop the unexplored field in which natural relationships between groups may be correlated with inherited physiological characteristics that are important in natural selection.

In a genetic analysis, one views the end results of gene action mostly as morphological differences. The genes initiate chains of little-understood physiological processes, which, in turn, lead to morphological differentiation. We may expect eventually to be able to link in an orderly manner the complex biological diversity observed in wild races with as yet unknown inherited physiological mechanisms.

THE DYNAMICS OF CLIMATIC RACES

The forms of *Achillea* growing in western North America present a picture of extreme morphological and physiological diversity. Almost every type of climate except the true desert has its race of *Achillea*. From analysis of the responses of the races in the very different climates of the transplant gardens and in the physiological experiments in the controlled greenhouses, it becomes obvious that each is particularly well fitted to the climate in which it is native. The fitness of the race is expressed both in its form and in its developmental processes, characters that are determined by the heredity of the plant.

The Achilleas along the central California transect afford an unusual opportunity for a study of the dynamics of natural populations and races. The local populations occur sufficiently close together to permit easy intermixture through dispersal of pollen and seed. The differences found between populations should therefore be due primarily to natural selection rather than to spatial isolation. All the population samples from this transect, taken at approximately 300-m. altitudinal intervals, were very variable. This fact tended to obscure the differences between the populations; yet, with the exception of those coming from similar environments, they were statistically and reactionally distinct.

INDIVIDUAL VARIABILITY

The variations in *Achillea* are found in all characters. Some of the variability is purely morphological and seems to have little selective value, because parallel variations, such as differences in length and width of the ligules of the ray florets, flower color (white or pink), leaf cut, herbage color, and branching pattern, occur in almost every population regardless of its original environment.

Other morphological characters have some correlation with the environment, for plants from similar environments are more or less alike. The inverse correlation between height of plant and altitude of habitat in the Sierra Nevada, and the positive correlation between depressed habit and extreme maritime habitat, have been brought out repeatedly in previous chapters. The thick leaf texture and intricate leaf cut of the most coastal plants are also correlated with environment, for inland the texture is appreciably thinner and the pattern more open. Size of heads and number of florets are generally greater in coastal forms than in those from farther inland and from mid altitudes.

Physiological characteristics directly influence the success of the plant in its native environment. Within limits, each population shows some individual variation in such characteristics as period of dormancy, time of flowering, frost resistance, and temperature and light requirements for maximum growth. Nevertheless, physiological characteristics are highly correlated with the kinds of climates in which the populations originate.

Different kinds of variation may be superimposed in the same individual, some being correlated with the environment, others not. It is those characteristics that are correlated with the environment that must be assumed to have survival value, but the correlation can be determined only after a sufficient number of individuals from different environments have been grown and studied.

Each local population of *Achillea* consists of a mixture of biotypes, and the composition of the mixture may vary somewhat in neighboring populations within the same climatic belt. But a distinct zonation of the biotype mixtures occurs as one passes from one climatic zone to the next, and this makes it possible to distinguish climatic races.

CLIMATIC RACES OF ACHILLEA

With the general picture of individual variability within local populations in mind, one can evaluate more clearly the characteristics of races from different climates. The two principal sequences of races studied— that of the transect across central California, with emphasis on an altitudinal series, and the latitudinal series extending from central California to Alaska—serve to illustrate the biological pattern in this complex. Additional information from northern European races fills in the picture.

THE CALIFORNIA TRANSECT. The hexaploid *Achillea borealis* extends from the coast of central California to the foothills of the Sierra Nevada. On that range and eastward it is replaced by the tetraploid *A. lanulosa*. Many races of these two species occupy the environmental niches along this transect.

Two races can be recognized on the coastal side of the outer Coast Range: a low, compacted, succulent maritime along the most exposed bluffs, and a taller, more open one from more protected localities. Their differences are hereditary, but the two races are nevertheless very similar physiologically. Both are well fitted to utilize the year-round growing season provided by their natural environment to build up slowly a bulky plant body. They grow vigorously, despite periods of frost, during the

winter, when abundant water is available, and continue at a dwindling rate during the summer and fall as water becomes scarcer. Their success depends primarily upon two sets of physiological characteristics: a capacity for year-round growth, and an ability to grow vigorously in the cool temperatures of the coast. Both utterly fail to survive in the Timberline garden, but persist indefinitely through the hot summers and rather cold winters at Mather, although they become winter-dormant there and grow with less vigor than at Stanford.

The populations of the foothill race, in the inner Coast Range and on both sides of the Great Valley, synchronize their growth closely with the seasons of their native environment, where lack of water during the summer is a more seriously limiting factor than it is in the coastal fog belt. This race grows during the cold, rainy winter like the coastal races, but it flowers earlier, thereby maturing completely before the dry season arrives, when higher temperatures initiate the drought-escaping summer dormancy typical of this race. It grows well at Stanford, but dies at Timberline. At Mather, it is considerably weaker than the coastal races, because the cold winter and hot summer force it into two periods of dormancy there.

The San Joaquin Valley race, exemplified by the Selma form from an environment marked by hot summers and ample soil moisture, utilizes these very favorable conditions to elaborate the largest plant body of any race. It has the ability to grow very vigorously under constantly high temperatures, as is shown by the experiments under controlled conditions, but its range of physiological tolerance permits it to succeed also at cooler temperatures, such as prevail in the garden at Stanford. Accordingly, under lowland conditions this race is very active during the summer and moderately active during the winter.

The races of *Achillea lanulosa* from the western slope of the Sierra Nevada form a graded altitudinal series that shows the close interrelationships between the physiological characteristics of the races and their environments. The race from the lower fringe of the coniferous forest where the January minimum temperatures seldom fall below freezing, as represented by the Groveland form from 915 m. altitude, remains winter-active and grows vigorously at Stanford, thrives reasonably well at Mather, but dies rather soon at Timberline.

Another race is found at Mather, at 1400 m. altitude in the heart of the *Pinus ponderosa* belt. This race from a climate with a longer and more severe winter is similar in many respects to the Groveland, but con-

tains a considerable proportion of winter-dormant types. Its representatives outperform all others in the Mather garden and are very adaptable, growing well under a wide range of conditions. Even at Timberline about 50 per cent of the individuals survive, although they are seldom· able to produce ripe seed there.

The race native in the *Abies* belt, where winters are longer and more severe, exemplified by populations from Aspen Valley at 1950 and Yosemite Creek at 2200 m., is strictly winter-dormant, even at Stanford. Its individuals attain their greatest and most rapid development under the warm days and cool nights at Mather. In the controlled greenhouse experiments also, its representative grew best under these temperature conditions, but it was less floriferous than plants from lower altitudes, unless stimulated by additional light. Individuals of this race survive fairly well and flower at Timberline, but they are susceptible to frost injury and rarely mature seed there.

A subalpine race in the zone of *Pinus Murrayana* is represented by three populations, Tenaya Lake, Tuolumne Meadows, and Timberline, at altitudes from 2500 to 3050 m. This high-altitude, short-season race has shorter, more slender stems with narrow, gray-pubescent leaves, and remains winter-dormant for a long time. Its individuals are not very vigorous at Stanford or at Mather, but grow well in the Timberline garden, where they are very resistant to frost and able to mature considerable seed. The experiments under controlled greenhouse conditions indicated that these forms require more light than· those from low altitudes.

An alpine race, represented by a population from Big Horn Lake at 3350 m. altitude, is the earliest-flowering, most frost-resistant, and shortest-stemmed of all the Sierran forms. It is the earliest to mature at Timberline, but in its more severe habitat among the snowy peaks it ripens seed only during the most favorable years.

On the eastern escarpment of the Sierra Nevada, in the more arid and highly continental Great Basin climates dominated by the sagebrush, *Artemisia tridentata,* races of *Achillea* are distinct from those at comparable altitudes on the western slope. Populations from Conway Summit at 2480 and Leevining at 2100 m. were studied, each having a shorter period of winter dormancy at Stanford than the alpines. They react as two distinct climatic races, the one from the higher altitude being shorter-stemmed and earlier-flowering than the other. In the temperature-controlled greenhouse experiments it was found that the Leevining race

developed rapidly and flowered with warm days and mild nights, conditions that prevail during the brief summer in its native habitat. In this behavior it resembles more the forms of *Achillea millefolium* from northern Europe than the other California Achilleas tried.

According to the experimental results, and with the present sampling, approximately eleven statistically distinct climatic races, or ecotypes, can be recognized from the 200-mile transect across central California. This is a much higher number of climatic races than has been found in any other plant group in an area of comparable size in any other part of the world.

Races from different latitudes. In addition to these climatic races from central California, there is clear evidence of the existence of others in the complex. The tetraploid *Achillea lanulosa* has invaded the mild climate of the coast redwood region in northern California and the Coast Ranges of Oregon, where it has evolved a winter-active race that parallels the tall coastal hexaploid race of *borealis* farther south. A tetraploid maritime race also occurs on exposed coastal bluffs in southern Oregon.

Achillea borealis has developed latitudinal races in western North America in addition to its races in California and Oregon. On Kiska Island, toward the western end of the Aleutian chain, a maritime, winter-active race can be linked morphologically with the one from the Oregon coast, but at Stanford it flowers a month earlier. A coastal race from Seward, Alaska, also ties in with this latitudinal series. It is early-flowering like the Kiska maritime, but is winter-dormant at Stanford. Physiologically it contrasts sharply with the coastal races from central California, for it thrives at Mather and survives at Timberline, and in the controlled greenhouse experiments it did not flower under any of the conditions. At higher altitudes on Kiska an extremely dwarf, early-flowering, winter-dormant race is found that differs markedly from the one at sea level, clearly showing within *borealis* the existence of altitudinal races that are reminiscent of the altitudinal series of *lanulosa* on the western slope of the Sierra Nevada.

Similar climatic races exist in the hexaploid European species, *Achillea millefolium*. Maritime and woodland races from Denmark were winter-active in California, and a subarctic race from Lapland was winter-dormant. All three are adapted for rapid development during the short but warm summers at these high latitudes, as is indicated by the experiments in the controlled greenhouses.

THE DYNAMICS OF NATURAL POPULATIONS

The analysis of the *Achillea* populations suggests that natural selection is far from being an absolutely rigid process. Many compromises are tolerated, and the fitness of a particular plant depends not so much upon a single character as upon a combination of several. Such a compensatory system of adaptation is flexible, for a relative lack of fitness in one character may be compensated for by special suitability in another. For example, an alpine that is susceptible to frost injury may succeed if it flowers early enough to mature some seed before the early frosts.

Among the races of *A. lanulosa* in the Sierra Nevada, that from Big Horn Lake represents the ultimate in adaptation to a short season, for it has the most favorable combination of characteristics for rapid development and resistance to frost. Nevertheless, it grows in so severe an environment that only in the most favorable years is it able to ripen seed. The high-altitude Kiska race of *A. borealis* has an additional adaptation for a short season, in that its rapidly flowering inflorescences are not produced on stems, but are almost sessile, thus reducing to a minimum the time required for development.

In a gradual climatic-altitudinal gradient, such as that of the western slope of the Sierra Nevada, genes may migrate comparatively freely. Abundant evidence shows that genes from one climatic zone infiltrate into adjacent zones. Examples have been cited in chapter III of individual plants that, having all the characteristics of their neighboring races, seem to have immigrated from a higher or sometimes a lower altitude. Their physiological range of tolerance has been sufficient to enable them to withstand the apparent change. Other individuals, having only one or two characters of a neighboring race, would seem to represent hybrid recombinations. Observations show that the immigrants or pioneers that invade another area do not supplant the indigenous members of the population there, since the differences between races from adjacent climatic zones are statistically significant even though genes continually infiltrate.

The newly established combinations encounter the force of natural selection, the eroding effects of which are doubtless most pronounced on those pioneers that have migrated too far from the environments to which they are most completely adapted. The local population, buffered by the physiological range of tolerance of its individuals and by the reservoir of genetic variability within it, has a considerable capacity to survive environmental changes. As long as the environment remains the same,

the race, in spite of constant immigration, retains its own identity through the dynamic equilibrium maintained by natural selection.

Physiologically the climatic races of *Achillea* are as distinct as species, and in certain cases the physiological differences between races of one species are greater than those between races of two related species. For example, the races of *A. lanulosa* in the Sierra Nevada differ more among themselves physiologically than the Leevining form of *lanulosa* differs from the northern European races of *millefolium,* all the latter forms being in rhythm with short, warm summers. The climatic race, like other kinds of ecotypes, is therefore the basic (but usually neglected) ecologic unit, just as the species is the basic taxonomic unit.

In their dynamic variability the climatic races that have been described are true counterparts of the ecotypes of Turesson. They and other ecotypic units are aggregates of similarly responding individuals and biotypes that are in rhythm with their environment. They are the result of the sorting and selecting effect of environment on all the potential biotypes of which their natural populations are composed. All have attained a degree of fitness for their environment that is reflected in the physiological and, to some extent, the morphological characters, both these kinds of characters being determined by heredity. Much discussion on terminology could be avoided if the dynamic concept of the ecological race were kept in mind.

ENVIRONMENTAL RELATIONS OF CLIMATIC RACES

The relationship between the climatic race and its environment may be clarified by analyzing the determining environmental factors and the basic functions of the green plant. The simple relationships shown diagrammatically in figure 27 summarize our conception of the climatic race in the evolutionary pattern of a species complex such as *Achillea*.

THE ENVIRONMENT. The environments of terrestrial plants are determined by climate, soil, and biota. Each of these elements can be determinative in evolution, with the result that climatic, edaphic, and biotic races are evolved. Climate is the basic factor of these three, since it largely determines the character of the other two. The study of the Achilleas has been simplified because the races investigated were primarily under climatic rather than edaphic or biotic influences, although soils and biota do play some role.

Climate, as a determining factor in environment, is the least complex of the three factors mentioned, since the elements determining it can be resolved into the simpler components of solar radiation, temperature, and

THE RECIPROCAL RELATIONSHIP BETWEEN THE ENVIRONMENT AND THE PLANT

ENVIRONMENT
(CLIMATE + SOIL + BIOTA)

THE GREEN PLANT

DETERMINING FACTORS

BASIC ENVIRONMENTAL REQUIREMENTS

Factors commonly limiting growth

Variables
governed by —
LATITUDE
ALTITUDE
GEOMORPHOLOGY

SOLAR RADIATION
TEMPERATURE
PRECIPITATION
SURFACE MATERIALS
AIR

LIGHT
SUITABLE TEMPERATURES
WATER
MINERAL NUTRIENTS
AIR

CHIEF DIFFERENCES IN
CLIMATES

CHIEF DIFFERENCES IN
CLIMATIC RACES

1. Relative intensities of determining factors.
2. Seasonal cycles.
3. Diurnal cycles.

1. Factor-intensity requirements
2. Seasonal periodicity
3. Diurnal periodicity
4. Form

PHYSIOLOGICAL AND
MORPHOLOGICAL
DIVERSITY
OF PLANTS

SPECIES SURVIVE environmental change
    through the ranges of tolerance of their individuals,
    populations, and races

SPECIES EVOLVE with changing environments
    through the diversity of their components

FIG. 27

precipitation. These, in turn, are primarily governed by latitude, altitude, and geomorphology.

Latitude is a factor of first importance in governing climate. It determines the amount of solar radiation received per unit area, thereby influencing temperature, air pressure, and the air currents so important for precipitation. The degree of contrast between the seasons and the relative lengths of days and nights are also largely determined by latitude.

Altitude, too, influences climate, because much of the radiant heat received from the sun is absorbed by the earth's surface, which, in turn, heats the atmosphere through convection currents. The thermodynamic equilibrium of the atmosphere results in a regular decrease in temperature with increases in altitude. The lowered temperature and air pressure at higher altitudes influence precipitation, and the relative density of the air influences the character of solar radiation received.

The morphology of the earth—the configurations and the positions, relative to each other, of land masses, oceans, and mountains—profoundly influences the movements of ocean currents and atmosphere, causing great differences in temperature and precipitation. The features of the earth's surface and the distance from the sea have strong effects on seasonal and diurnal cycles, resulting, for example, in the well known differences between maritime and continental climates. These features grade down to small variations in the earth's relief that create innumerable microclimates.

The relative amounts of solar radiation, temperature, and precipitation distributed over daily and seasonal periods determine the climates of the earth. From a knowledge of these values for a given locality, its climate can be fairly accurately characterized.

BASIC REQUIREMENTS OF PLANTS. The three principal variables that determine climate also primarily regulate the growth of green plants. In addition, mineral nutrients and air are necessary for plant growth. Plants differ from one another, as indicated in figure 27, in the relative amounts of these factors required (the factor-intensity requirements), in seasonal and diurnal periodicities, and in form. These differences in plants, excepting form, have their counterparts in the chief differences between climates. It is the variation in these requirements that is reflected in the differences between climatic races.

Factor-intensity requirements frequently differ between climatic races. The coastal forms of *Achillea,* for example, thrive at lower temperatures than the race from the San Joaquin Valley. Also, the high-altitude races

of *A. lanulosa* require for their full development more light than those from lower altitudes, as was seen in chapter IV.

Seasonal periodicity is one of the most important characteristics that fit the races to their respective climates. In most environments the basic requirements for plant growth are not realized throughout the entire year, and perennial plants must therefore synchronize their growth with the seasons in order to survive. They do not grow at the same rate throughout the year and usually have a dormant period to coincide with the season unfavorable for growth. In some climates dormancy is enforced by freezing temperatures in winter, in others by high temperatures or lack of moisture in summer. The matching of the seasonal cycles of the contrasting climates along the California transect with the periodicities of the *Achillea* races is a striking example of interrelationship between climate and plant.

Diurnal periodicity plays an important physiological role in plant growth. The experiments in the controlled greenhouses demonstrated profound differences in the diurnal periodicity of the *Achillea* races through their responses to variations in day and night temperatures. The importance of this periodicity for various climatic races was discussed in chapter IV.

Went (1944), who proposed the term *thermoperiodicity* for diurnal temperature periodicity, has demonstrated, through extensive experiments under controlled conditions, significant differences in the thermoperiodic requirements of varieties of tomatoes. In some varieties these requirements change considerably as the plants approach maturity. Optimum growth under such a pattern of periodicity can obviously take place only in an environment with a corresponding seasonal progression in temperatures. Such an example emphasizes the intimate relationship between plant and climate.

Photoperiodicity is a diurnal periodicity with duration of light as the variable. The extensive literature on photoperiodicity is replete with examples of the importance of day length in the growth and development of plants. Olmsted (1944) found significant differences in the day-length requirements of samples of the side-oats grama, *Bouteloua curtipendula* (Michx.) Torr., originating over a series of latitudes from southern Texas to North Dakota. The more northern strains required longer days for flowering than the southern, but there was considerable variation in response among individuals from intermediate latitudes. The differences between strains from southern and northern latitudes indicate the presence of climatic races, and the variability within the samples shows that each population is composed of a mixture of biotypes.

Form differs widely in climatic races, as can be seen from figure 1 (pp. 6, 7). The giant Achilleas grow where conditions are the most favorable, with sufficient water, fertile soils, and long seasons, as in the bottom lands of the San Joaquin Valley and on the coastal side of the Coast Range. The dwarf types, on the other hand, grow in alpine environments with short summers, as in the Sierra Nevada and on Kiska Island.

In order to give a visual impression of the magnitude of the differences observed, two pairs of the most strikingly different races of *Achillea* and one pair of the least are compared in figures 28 to 30. These plants were photographed as they grew in the garden at Stanford.

In figure 28 contrasting climatic races belonging to different species of one species complex are compared. One is a maritime race of *A. borealis* from Bodega and is active the year round; the other, an alpine *lanulosa* from Big Horn Lake, is winter-dormant. The graphs in the upper part of this figure show the monthly ranges between the average maximum and minimum temperatures recorded at weather stations near the habitats of these forms. These graphs reflect the differences in temperature between a mild, equable, maritime climate and a cold, continental one at high altitude with marked seasonal and diurnal changes.

Figure 29 shows an even more striking morphological contrast, in this case between two races of one species, *A. borealis*. A plant of the giant San Joaquin Valley race from Selma, California, adapted to grow through a long warm season and one of the latest forms to flower at Stanford, is shown beside a plant from Seward, Kenai Peninsula, Alaska. The Seward plant is winter-dormant at Stanford, but develops so quickly in spring that it flowers two months ahead of the Selma form. The graphs show that the characteristically warm temperate, continental climate at Fresno and the maritime one of a latitude 24° farther north at Seward, with great seasonal but little diurnal variation, are so different that there is no overlapping in the ranges of their temperatures.

A third example, shown in figure 30, contrasts with the two preceding ones and illustrates neighboring climatic races of one species, *A. lanulosa*. The two plants came from the western slope of the Sierra Nevada, one from Groveland at 915 m. altitude, the other from Mather at 1400 m. The average monthly temperature difference between the two habitats is less than 2° C., but Mather has four months during which the mean minimum temperatures are below the freezing point, and the growing season there is 48 days shorter than at Groveland. In the Stanford environment the two plants look alike, although during the winter the Groveland form remains active and this Mather individual is dormant. At Mather, however, the Mather race is considerably the taller, as is shown by the graph
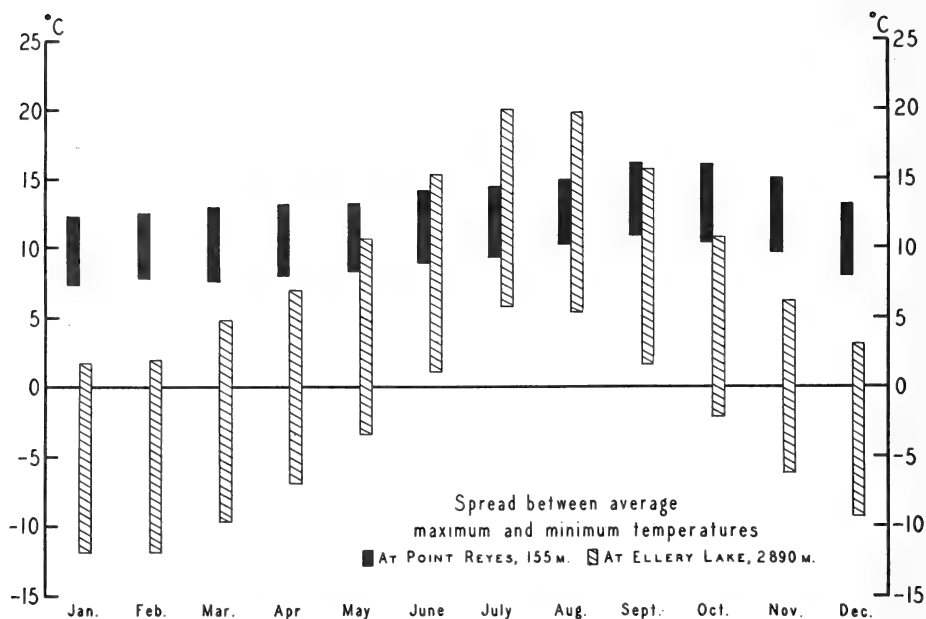
FIG. 28. Contrast between a coastal and an alpine race of *Achillea,* and the approximate temperature ranges of their native habitats.

A maritime race of *Achillea borealis* from the Bodega coast of central California (left) and an alpine race of *A. lanulosa* from Big Horn Lake at 3350 m. elevation in the Sierra Nevada (right) growing in the Stanford garden and reproduced to the same scale.
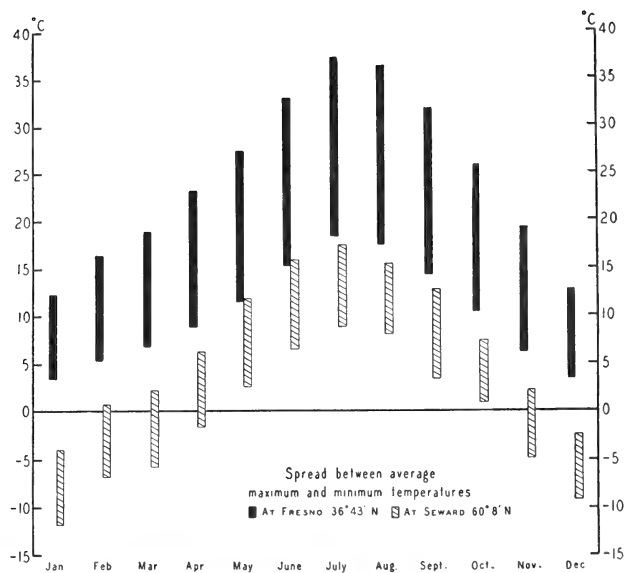
FIG. 29. Contrast between a southern and a northern race of *Achillea borealis,* and the approximate temperature ranges of their native habitats.

A race from Selma, California, at 36° 31′ north latitude (left) and another from Seward, Alaska, at 60° 8′ north (right) growing in the Stanford garden and reproduced to the same scale.
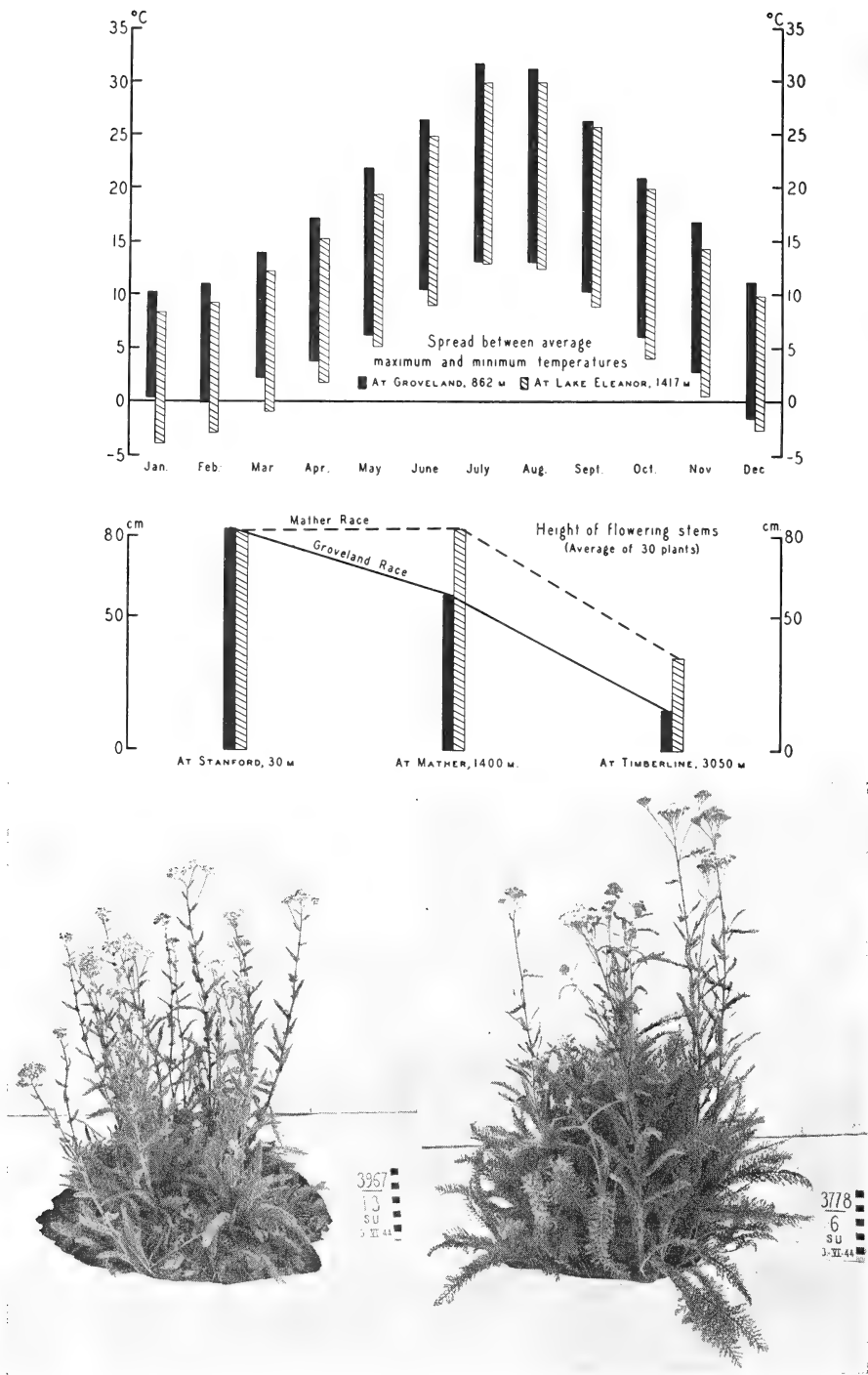
FIG. 30. Morphologically similar but reactionally distinct races of *Achillea lanulosa* from neighboring altitudes in the Sierra Nevada, and the approximate temperature ranges of their native habitats.

A race from Groveland at 915 m. elevation (left) and another from Mather at 1400 m. (right) growing in the Stanford garden and reproduced to the same scale. The center graph illustrates the differences in reaction at the three transplant stations.

of stem heights in the center of the figure. A similar difference in size between the races occurs at Timberline, where the Mather race also survives a great deal the better. The individual variation within these populations tends to obscure the racial differences so that statistical studies are needed to distinguish them—a method that was not required in the two preceding examples because the differences between those races are obvious.

These three examples illustrate some of the kinds and degrees of differences to be found between climatic races of a species complex. They also indicate the approximate upper and lower limits of diversity distinguishing the races of the present material, although the Kiska alpine race is tinier than the Seward. Similar, although usually less spectacular, differences may be found in all plant groups containing ecotypes.

OTHER STUDIES ON ECOLOGICAL RACES

CLIMATIC RACES. The most extensive studies on climatic races have been made by Turesson (1922, 1925, 1930), who, using many different species, reported numerous examples of maritime, inland, foothill, subalpine, alpine, and latitudinal races. One of the present authors (Clausen, 1922) determined the existence of maritime and inland climatic races in *Viola tricolor* from Denmark, and described (1926, pp. 16–22) the genetic differences between these races. The studies of Gregor (1938, 1939) on *Plantago maritima* L. from Great Britain, the Faroe Islands, Iceland, and Greenland have shown the existence of climatic races in that species. He also presented statistical data describing the variability of population samples. Lawrence (1945) has reported that *Deschampsia caespitosa* (L.) Beauv., one of the most widely distributed grasses in the world, also is composed of series of climatic races, both altitudinal and latitudinal. Olmsted, as was mentioned, has demonstrated the presence of latitudinal races in *Bouteloua curtipendula* that differ in their day-length requirements. A parallel example has been investigated by Goodwin (1944) in the seaside goldenrod, *Solidago sempervirens* L.: a southern race from Florida is taller and much later-flowering than races from more northern habitats in Maryland and Massachusetts when all are grown in the same environment at Rochester, New York. These differences between latitudinal forms of one species of *Solidago* depend upon a series of genes, as has been demonstrated by the character of segregation in second-generation offspring from controlled crossings. Many other examples from the flora of western North America have been reported by the writers (1940), but none of these species has as complete a series of races as *Achillea*.

An example of seasonal ecotypes is found in *Lamium purpureum* L., which has both summer annual and winter annual races growing in the same area (Müntzing, 1932). Plants of the summer annual race germinate in early spring, flower after six weeks, and then die. If sown in the fall they may flower before winter, but in all events are winter-killed. The winter annual race germinates in the fall and develops a rosette, with which it winters over, then flowers in the spring and dies. It does not flower at the same time as the summer annual form if sown in the spring, but continues in vegetative growth until the following spring, and then flowers. The over-wintering appears to be necessary for the flowering of this race. An F_2 hybrid population between the two races showed segregation in this physiological character of periodicity. The seasonal dimorphism in these two physiologically very different races of *Lamium purpureum* provides an interesting example of a species that has evolved two distinct patterns of seasonal periodicity that fit the same northern European climate.

Examples of climatic races have also been found in the animal kingdom. One of the earliest recorded is that of the deer mouse, *Peromyscus maniculatus,* a species that occurs over most of North America and has developed some twenty-five distinct geographic subspecies. These subspecies interbreed in captivity. Sumner (1924) demonstrated that two of these subspecies or races from climatically contrasting environments remained distinct for from six to ten generations when reared in a uniform environment different from either of those from which they came. One of these races was the dark-colored, long-tailed ssp. *rubidus* from the northern California coast, and the other was the lighter-colored, short-tailed ssp. *sonoriensis* from the Mohave Desert of California.

Moore (1942) has demonstrated the existence of similar climatic races in the American meadow frog, *Rana pipiens,* through experiments in which a race from the Gulf states was found to require a higher range of temperatures for the development of embryonic stages than a race from New England whose eggs are deposited in ponds with lower temperatures.

Goldschmidt (1934, pp. 133–136) has shown that in the moth *Lymantria dispar* there are significant differences in the incubation time of races from different climates in Asia and Europe. Hovanitz (1944) has demonstrated the presence of parallel color mutations in the closely related alfalfa butterfly (*Colias eurytheme*) and clover butterfly (*C. chrysotheme*), which are linked with physiological characters that separate latitudinal climatic races within these species.

EDAPHIC AND BIOTIC RACES. Although climatic factors are of primary importance in the environment and largely determine the conditions under which the organism must live, soils and biotic factors are also important. Some interesting examples are on record of races of plants and animals that show correlations with the edaphic and biotic factors of their environment.

True examples of edaphic races of one species are infrequent in the literature. In *Hieracium umbellatum* L., Turesson (1922, pp. 334–340) pointed out the edaphic correlations of several forms. In addition to the tall inland type in southern Sweden, three recognizable races alternate along the coast. One on exposed cliffs is late-flowering, broad-leaved, succulent, and depressed; another on shifting sand dunes is narrow-leaved and erect; and the third, on stationary dunes, is narrow-leaved but prostrate. The third type is not found on the moving sand, by which it would be quickly covered. Some crossing between the races apparently takes place, as recombination types were found. A similar edaphic differentiation probably exists among the extreme coastal Achilleas of California, for, as was mentioned in chapter II, populations from well drained dunes are earlier-flowering in the Stanford garden than those from the adjacent clay bluffs.

Gregor (1938) has described ecotypes in *Plantago maritima* L. from salt marsh, waterlogged coastal mud, drained coastal mud, grassland above the high-tide mark, and exposed sea cliff. The first three are apparently due to edaphic factors, but the last two are probably not due solely to these, for the ecotype from the grassland has been influenced by the biotic factor of grazing, with a greater survival of the more decumbent types in heavily grazed habitats, and the one from the sea cliff may have resulted in part from the action of wind.

A similar genetic differentiation into prostrate, decumbent, and erect forms was observed in populations of the diploid *Phleum nodosum* L. and the hexaploid *P. pratense* L. (Gregor and Sansome, 1930; Gregor, 1931). The more decumbent forms are found mainly in fields used habitually for grazing, and the erect ones mainly in fields used for hay crops. Evidently the influence here is primarily biotic and agricultural.

Zherebina (1930–1931) found edaphic ecotypes superimposed upon climatic races in *Bromus inermis* Leyss. In the more northern regions of Russia and Siberia there are edaphic ecotypes for river bottom lands and for loose, sandy soil, and to the southward, steppe ecotypes. In the Altai Mountains a subalpine ecotype has been differentiated at colder altitudes, and low-altitude ecotypes exist for moist valleys and for rocky slopes.

Sumner (1926, 1930) studied three subspecies of the beach mouse, *Peromyscus polionotus,* native to Florida and adjacent states. These are distinguished by pelage color and are completely interfertile. One very pale, almost white subspecies, *leucocephalus,* lives on the white sands of Santa Rosa Island just off the northwest coast of Florida. Another, a dark-buff subspecies, *polionotus,* is found on dark clay soils of the mainland interior. The third subspecies, *albifrons,* of an intermediate shade, lives on medium-colored soils in a region some 40 miles wide between the areas of the other two. Its populations become gradually darker as the distance from the sea increases, but they are replaced rather abruptly by the still darker populations of the interior subspecies, with only a narrow zone of intergradation. The direct correlation between pelage color and color of soil suggests that the three subspecies are protectively colored edaphic races. Sumner showed that the genetic basis of their differences was not very complicated, for good counterparts of the parental races were obtained in the F_2's and in backcrossings. Dice and Blossom (1937) noted many similar color correlations between races of various mammalian species and the soils of their habitats.

In the stickleback fishes, *Gasterosteus aculeatus* L., Heuts (1947) has found distinct physiological differences between fresh- and salt-water races. In Belgium, the fresh-water race is the smaller of the two, and, instead of scales, has less than 10 bony plates; the salt-water race is larger and has around 30 to 36 plates. The rather abrupt change in salinity as the rivers reach the sea is correlated with a similar abrupt change in the stickleback populations, but some morphological intergrades occur in the transitional zone. The eggs of the fresh-water race hatch well in fresh water but poorly in brackish, and those of the salt-water race, which migrates to brackish water for spawning, hatch well in brackish water but poorly in fresh. The hatching percentage of the two races is also unequally influenced by temperature. Accordingly, the two variables of salinity and temperature act as selective agents in maintaining two edaphic races, often in neighboring waters. The morphological intergrades between the two belong either to one physiological type or to the other. The two races can be intercrossed under proper combinations of salinity and temperature where both will survive; under such conditions there is little selection, and many morphological intermediates arise, but even here offspring comparable to the parental races are the more common. It is evident that the two forms belong to one species, that they constitute two edaphic races adapted to different ranges of salinity, that the differences are determined by genes in a complex system favoring the parental forms, and that there are several physiological mechanisms that tend to keep the races distinct.

The most thoroughly investigated example of biotic influence in the development of races in plants is found in the flaxweed, *Camelina sativa* (L.) Crantz. Tedin (1925) showed that the races of this species that grow as weeds in flax fields resemble flax in habit, period of development, and seed size. Those that grow with other crops differ genetically. Sinskaia and Beztuzheva (1930–1931), making a thorough analysis of the forms found in the U.S.S.R., pointed out that the flaxweed imitates the race of flax with which it grows in its developmental period, height, thickness of stem, branching, and degree of leafiness. Moreover, these characters vary both in flax and in *Camelina* in parallel fashion, according to a zonal succession; thus in the south the flax and the *Camelina* with it are of shorter stature and earlier in development than the races of both plants found in the north. Here, then, is climatic differentiation superimposed upon biotic adaptation. Sinskaia (1930–1931) reported ecotypes in another weed of agricultural crops, *Brassica nigra* (L.) Koch, that, like the *Camelina* ecotypes, are the result of unconscious selection by man; and in them, too, both climatic and biotic selective factors play a role.

CONCLUSIONS

The investigations on *Achillea* disclose phases of the intricately balanced equilibria that exist between plants and environment. They also provide a rough measure of the relative intensity of the environmental differences which lead to the appearance of statistically detectable climatic races. Some of the mechanisms by which plants are fitted to available environments have also been uncovered in these studies. From the results a few generalizations may be drawn.

The ecological race approaches an equilibrium with its environment. This equilibrium is maintained by the force of natural variation inherent in the organism balanced against the force of natural selection operating through environmental factors. Such an equilibrium is dynamic, and accordingly somewhat flexible. The ecological race maintains its flexibility through the actual and potential morphologic and physiologic diversity of its various components. This diversity provides it with a powerful means of adjusting itself to changing conditions. It assures the continuity of the species, even though the composition of its races may change in the process.

To become widespread, a species must develop many ecological races. These arise through natural selection in response to determining factors of the environment—some in response to climatic factors, others to edaphic or biotic factors. Each ecological race differs genetically from the others.

Often races develop through the effects of two or more selective factors' being superimposed upon one another.

Climatic races have arisen in response to different climates. Their most important characteristic is the ability to synchronize their activities with the diurnal and seasonal periodicities of their environments. Even relatively small climatic differences may result in statistically detectable differences between races. The rigors and advantages of extreme environments may result in the selection of growth forms and physiological patterns of a specialized nature, but the resultant races prove to be remarkably well adapted to those environments. The tiny alpine of the higher altitudes on Kiska Island and the giant race from the San Joaquin Valley may be taken as contrasting examples.

Each climatic race consists of many local populations possessing in common those characteristics essential for survival in their particular environmental zone. Similarity in essential characteristics does not preclude individual variability. No two populations are identical in composition, and they are composed of individuals scarcely two of which belong to the same biotype. Although the individuals and populations vary, the races are statistically and reactionally distinct.

The fitness of the race to its environment depends upon the fitness of its individual members. Some individuals within the race are better fitted than others, but each one has a physiological tolerance that enables it to survive over a range of conditions, and thus meet changes that may occur in its surroundings. The fitness of the race is an approximation, and probably few races ever fit their natural environments precisely.

Changes in the ecological race occur under pressure of changes in the environment. As some biotypes are eliminated by natural selection, the race gradually changes. New biotypes built from the genes of old ones are constantly made available to the selective processes through the migration and exchange of genes. In *Achillea,* with its rather continuous distribution and ready dispersal, there is considerable circumstantial evidence of invasion and gene exchange between climatic races. Gene mutation is another source of variation to be considered.

The variability and diversity in certain groups of plants are so great that they become difficult to comprehend. In the Achilleas, at least eleven diverse climatic races were found along a 200-mile transect across central California, each race including a vast amount of variability. The *Achillea millefolium* complex has been able to inhabit most of the environments in the Northern Hemisphere. The samples taken outside central Cali-

fornia suggest that the total number of ecological races within its three species may easily run into the hundreds.

The evolutionary history of these Achilleas is still unknown. Their species form an incomplete polyploid complex with 9 as the basic chromosome number, but only 18- and 27-paired species have been discovered. These tetraploid and hexaploid forms, which are presumably derived, are very aggressive, and they may have already displaced their unknown diploid ancestors. Although the sampling has been relatively dense in the western United States where tetraploids and hexaploids meet, there is a chance that rare diploids still exist here.

Many problems basic to the understanding of climatic races still remain unexplored. Among these are: the inheritance and gene basis of those physiological characteristics that determine the fitness of the race for the climate; the manner in which the environment acts as a selective and sorting agent in populations of hybrids between races from contrasting climates; and the balance relations between the gene-controlled physiological processes that distinguish the climatic races. Meanwhile, the more general evidence now available suggests promising directions for future study.

LITERATURE CITED

Clausen, J. 1922. Studies on the collective species *Viola tricolor* L. II. Bot. Tidsskrift 37:363–416.

—— 1926. Genetical and cytological investigations on *Viola tricolor* L. and *V. arvensis* Murr. Hereditas 8:1–156.

—— David D. Keck, and William M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. Wash. Pub. 520. vii + 452 pp.

Dice, Lee R., and Philip M. Blossom. 1937. Studies of mammalian ecology in southwestern North America with special attention to the colors of desert mammals. Carnegie Inst. Wash. Pub. 485. iv + 129 pp.

Goldschmidt, Richard. 1934. *Lymantria*. Bibliographia genetica 11:1–186.

Goodwin, Richard H. 1944. The inheritance of flowering time in a short-day species, *Solidago sempervirens* L. Genetics 29:503–519.

Gregor, J. W. 1931. Experimental delimitation of species. New Phytol. 30:204–217.

—— 1938. Experimental taxonomy. II. Initial population differentiation in *Plantago maritima* L. of Britain. New Phytol. 37:15–49.

—— 1939. Experimental taxonomy. IV. Population differentiation in North American and European sea plantains allied to *Plantago maritima* L. New Phytol. 38:293–322.

—— and F. W. Sansome. 1930. Experiments on the genetics of wild populations. II. *Phleum pratense* L. and the hybrid *P. pratense* L. × *P. alpinum* L. Jour. Genetics 22:373–387.

Heuts, M. J. 1947. Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. Evolution 1:89–102.

Hiesey, William M., Jens Clausen, and David D. Keck. 1942. Relations between climate and intraspecific variation in plants. Amer. Naturalist 76:5–22.

Hovanitz, William. 1944. The ecological significance of the color phases of *Colias chrysotheme* in North America. Ecology 25:45–60.

Lawrence, William E. 1945. Some ecotypic relations of *Deschampsia caespitosa*. Amer. Jour. Bot. 32:298–314.

—— 1947. Chromosome numbers in *Achillea* in relation to geographic distribution. Amer. Jour. Bot., vol. 34.

Moore, John A. 1942. The role of temperature in speciation of frogs. Biological Symposia 6:189–213.

Müntzing, Arne. 1932. Untersuchungen über Periodizität und Saison-Dimorphismus bei einigen annuellen *Lamium*-Arten. Botaniska Notiser, pp. 153–176.

Olmsted, Charles E. 1944. Growth and development in range grasses. IV. Photoperiodic responses in twelve geographic strains of side-oats grama. Bot. Gaz. 106:46–74.

Sinskaia, E. N. 1930–1931. The study of species in their dynamics and interrelation with different types of vegetation. Bull. Appl. Bot., Genet., and Plant Breed. 25:50–97.

—— and A. A. Beztuzheva. 1930–1931. The forms of *Camelina sativa* in connection with climate, flax and man. Bull. Appl. Bot., Genet., and Plant Breed. 25:98–200.

SUMNER, FRANCIS B. 1924. The stability of subspecific characters under changed conditions of environment. Amer. Naturalist 58:481–505.

——— 1926. An analysis of geographic variation in mice of the *Peromyscus polionotus* group from Florida and Alabama. Jour. Mammal. 7:149–184.

——— 1930. Genetic and distributional studies of three sub-species of *Peromyscus*. Jour. Genetics 23:275–376.

TEDIN, OLOF. 1925. Vererbung, Variation und Systematik in der Gattung *Camelina*. Hereditas 6:275–386.

TURESSON, GÖTE. 1922. The genotypical response of the plant species to the habitat. Hereditas 3:211–350.

——— 1925. The plant species in relation to habitat and climate. Hereditas 6:147–236.

——— 1930. The selective effect of climate upon the plant species. Hereditas 14:99–152.

WENT, F. W. 1943. Plant growth under controlled conditions. I. The air-conditioned greenhouses at the California Institute of Technology. Amer. Jour. Bot. 30:157–163.

——— 1944. Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of the tomato. Amer. Jour. Bot. 31:135–150.

ZHEREBINA, Z. N. 1930–1931. Essay of a botanical-agronomical study of awnless brome grass (*Bromus inermis* Leyss.). Bull. Appl. Bot., Genet., and Plant Breed. 25:346–351.

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